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Responses to optic flow in the ventral intraparietal area

Responses to optic flow in the ventral intraparietal area.

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About the corners of the pages

When turned in rapid succession, the corners of the odd pages show a oscillating diverging optic flow pattern The dot pattern oscillates four times with a period of 16 double pages The lifetime of the dots is 10 double pages A similar stimulus was used to test for example neuron J7 5 (see chapter 5)
When turned in rapid succession, the corners of the even pages show the vector field of fanning (compare with fig 3 1) One can easily observe the rotation axis of the frontoparallel plane The lifetime of the dots is again 10 double pages

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Chapter 1

General introduction and summary

1.1 Introduction

Movement is an important aspect of the visual world The brain processes movement in numerous ways and on several levels The highest and probably most complex level is the cognitive system It interprets the continuous input of information and based on previous input, acts on it Furthermore it plans ahead, by trying to predict future events (obstacles) and to find the best strategy for dealing with them

This thesis presents a study on a small area of the brain called VIP (Ventral Intra-Parietal area) which is involved in the processing of movement (direction, velocity and possibly also acceleration and deceleration) One could argue that the level of information processing is on the level of a direct response to an event (movement) However, some arguments will be presented to put this area a small step higher on the complexity hierarchy of the brain, by showing that this area is acting differently to stimuli depending on the (very near) past

VIP, the area of interest, lies in the visual cortex A large part of the brain of humans and monkey's is devoted to the processing of visual information The complexity of the input is high Subjects move through the outside world and objects move in it Therefore the visual input on our retina is always changing Evolution has provided us with means to stabilize images by making compensating eye, head and body movements Nevertheless, most of the visual input will continuously change in time

When detecting a moving object, it is not necessary to observe the nature of the object before determining where it is going Psychological studies have already established that object recognition (what) and object motion (where) are processed separately in the brain Head and eye movements induce a well-defined changing visual pattern on our retina (further on called optic flow) If the outside world is stable while performing that movement, this optic flow pattern has a clear relation with the shape of the outside

world and the movement we made Psychophysical experiments have shown that we can estimate our movements in a unique way from such an optic flow field Psychophysical experiments have also shown that there exists a complex interaction between gaze direction and our postural response to simulated moving environments (Gielen and van Asten, 1990) The combination of psychophysiology and electrophysiology methods showed that there is attention modulation of visual motion processing (Treue and Maunsell, 1996) We can estimate the shape of an object based on the optic flow field it generates on our retina (Dijkstra et al , 1994b) Both tasks, shape from motion and egomotion detection, can not be done simply by looking at the moving patterns on the retina For example, it can be shown mathematically that one can not distinguish a slowly moving object close to us, from a faster moving object further away, when one uses only one eye Also, certain shapes generate an optic flow pattern that is not unique to that particular shape Under natural conditions this is merely a small handicap For dealing with objects nearby, we have binocular vision to make an accurate estimate of the distance and the three dimensional shape of an object Structure of the object, texture, shade and color give us more information about objects, surround and light conditions Our memory helps us to solve ambiguities (a nice example is the rotation of a hollow mask of half a face, which always is perceived looking towards you if it rotates, even if the nose is pointing away from you) Non-visual senses help the visual system to increase its performance Vestibular input gives information about head accelerations, proprioceptive input gives information about body orientation and eye position Further, somatosensory cues tell about movement (air flow) sound gives information of our relative location with respect to the source, direction of movement and because of echoes, a sense of size and structure of a room, etc

This thesis will touch upon some of these other modalities, but the prime subject will be optic flow What are the properties of neurons in VIP involved in analyzing optic flow?

1.2 Movement detection

Motion is, physically described, a spatial change over time To detect motion one needs at least two measurements separated by time and space Reichardt's motion detector (1961) is a elegant implementation of this principle (Fig 1 1) Two different photoreceptors (D1 and D2) at a distance dx of each other, are projecting to a summation unit M One of the photoreceptors projects without delay to unit M, the other with a delay dt If a pattern travels over the retina in the preferred direction of the detector, it would stimulate the delayed unit first, its signal would reach the summation unit M with the delay dt If the pattern moves continuously in the preferred direction and reaches the non-delayed photoreceptor after time dt, its output reaches unit M at the same time as the signal from the delayed photoreceptor This would evoke the maximal response in unit M Every other speed (dx/dt) of the pattern would result in a lack of coincidence of signals in unit M, and therefore in a less optimal response

The interaction of spatial summation and temporal integration can work indepen-

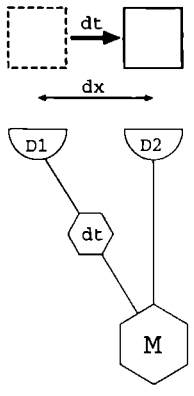


Figure 1.1: *Schematic drawing of a Reichardt's motion detector. Two photoreceptors (D1 and D2) at a distance dx of each other, are projecting to a summation unit M. One projection is delayed by a delay unit for a period dt. The optimal stimulus moves from left to the right in time dt, as indicated by the two squares.*

dently under a wide range of conditions (Fredericksen et al., 1994b). Using a random pixel array (spatiotemporally broad-band) apparent motion stimulus designed to isolate specific populations of visual motion detectors, Fredericksen et al., (1994) showed that on the level of human motion perception one can determine the basic dimensions of the selected motion detector population's receptive field. At the neural level there is a clear hierarchy in the sophistication of neurons in detecting movement (or optic flow) features within their receptive fields. Consider for example the aperture problem. A change in direction relative to the alignment of both receptors can be compensated by a change in speed for a simple motion detector as described above (Fig. 1.2). The detector measures only the speed relative to both detectors. If the stimulating pattern is large relative to the size of the receptors, both receptors can be stimulated by different parts of the pattern (Fig. 1.2, left). In that case the effective distance (dx') traveled by the stimulating pattern is smaller than dx, the distance between the receptors. This would thus result in a wrong estimate of the speed for a non-receptor-aligned direction. Using plaid stimuli, Movshon et al., (1985) showed very elegantly that neurons in area V1 suffer from this aperture problem. In area MT on the other hand, by integrating input from several V1 neurons, the brain is able to resolve the aperture problem. Cells in area MT can therefore respond correctly to the direction of a moving plaid, instead of having different optimal direction profiles at different speeds.

The correspondence problem is another problem that the brain faces while measuring local movements. In the simplest case, consider a random dot scene, where each dot moves in a random direction. Present only two instances of this frame with a time interval dt. Which dot belongs then to which dot and thus what is the direction of movement for every dot? Clearly the brain has to make assumptions about the scene it

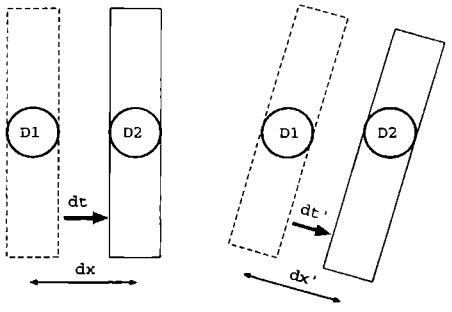


Figure 1.2: *Schematic drawing of the aperture problem. In both the right and left graph, two photoreceptors (D1 and D2) at a distance dx of each other, are stimulated by a moving bar. See text for further explanation.*

observes. There are several factors that impose restrictions on the solution. In general, one assumes that the number of dots remains constant and that there is a maximum speed for the dots. The scene will be analysed under the hypothesis that the dots closest to each other in both frames have the best chance of being the same one. Furthermore, dots are likely to form an object, so grouping dots which move in the same direction could help to solve ambiguities. In everyday life this problem is not a big one since there are a lot of clues to connect elements over time. Moreover, movements tend to be smooth and thus predictable. However in experiments where one uses moving dots with a lifetime of 332 msec which are updated at a 60 Hz frame rate, we have to be at least aware of the correspondence problem.

Optic flow

A general description of a flow field consists of flow vectors, indicating the movement at each location in the visual field. The length of a flow vector indicates the speed of the optic flow, the direction of the vector represents the direction of the flow. The horizontal and vertical optic flow speed at the position (x, y) can be described by $u(x, y)$ and $v(x, y)$, respectively. An optic flow field can then be represented as:

$$\vec{f}(x, y) = \begin{pmatrix} u(x, y) \\ v(x, y) \end{pmatrix} \tag{1.1}$$

In a first order approximation we can express the horizontal and vertical components of optic flow in a constant part (translation $\vec{T}$ or u_0 and v_0) and a part depending linearly on the position (A, B, C, D). A complete description leaves us then with $u_h(x, y)$ and $v_h(x, y)$, describing the second and higher order terms $(x^2, xy, xy^2, ...)$ of the flow field:

$$u(x, y) = u_0 + Ax + By + u_h(x, y) \tag{1.2}$$

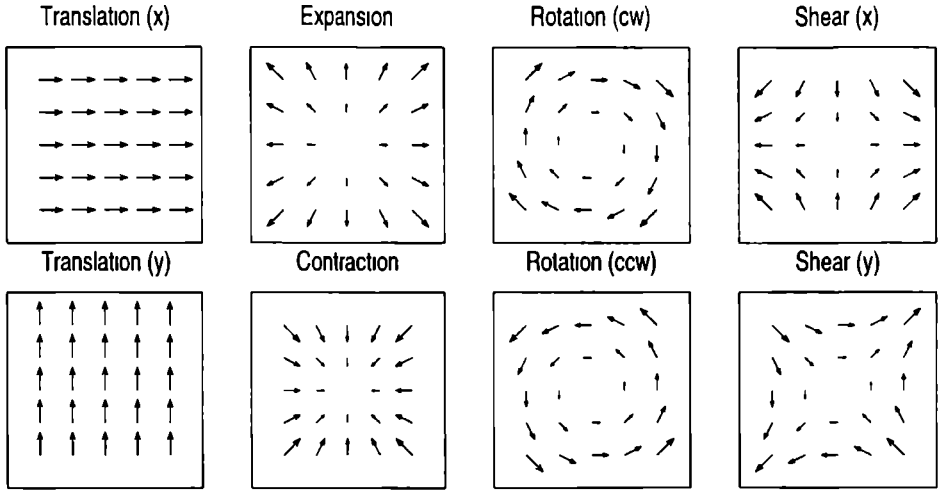


Figure 1 3 *Zeroth and first order optic flow components*

$$v(x,y) = v_0 + Cx + Dy + v_h(x,y) \tag{1 3}$$

A flow field can be decomposed uniquely in one zero and three first order terms (Koenderink and van Doorn, 1975) which are orthogonal, and a remaining term $\vec{f}_h$ which describes the higher order terms of the flow field

$$\vec{f}(x,y) = \vec{T} + \vec{D} + \vec{R} + \vec{S} + \vec{f}_h \tag{1 4}$$

Here $\vec{T}$ stands for Translation, $\vec{D}$ for Divergence (expansion and contraction), $\vec{R}$ for Rotation (clockwise or counter clockwise) and $\vec{S}$ for Shear (or deformation) In figure 1 3 is shown what is meant by Translation, Divergence, Rotation and Shear

Movement in the real world can give rise to very complex optic flow fields with large numbers of higher order terms (Subbarao, 1989) In a first approximation we will limit ourselves to the simple case of a moving plane The movement of a camera or a subject relative to a surface generates an optic flow pattern on the image plane of the camera or retina (Fig 1 4) We describe this movement by the two vectors $\vec{V}, \vec{\Omega}$, where $\vec{V}$ describes a translation and $\vec{\Omega}$ a rotation in the 3D space (with X Y Z as coordinate axis) If we approximate a section of this surface by a plane $Z = pX + qY + n$, we can calculate the optic flow generated by this movement on the projection plane

$$u(x,y) = u_0 + Ax + By + (Ex + Fy)x \tag{1 5}$$

$$v(x,y) = v_0 + Cx + Dy + (Ex + Fy)y \tag{1 6}$$

where A, B, C, D, E and F are constants depending on the orientation (p,q) and movement $(\vec{V}, \vec{\Omega})$ of the plane Notice that the distance to the plane is not essential at

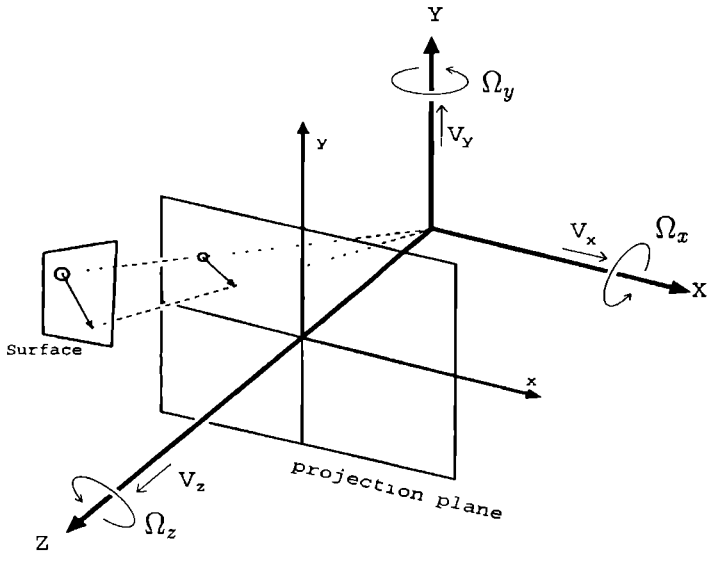


Figure 1.4: *Schematic drawing of the projection of a 3D surface (X, Y, Z coordinates) on a projection plane (x,y coordinates). The projection plane can move relative to the surface by translation ($V_x V_y V_z$) and rotation ($\Omega_x \Omega_y \Omega_z$). The projection of an arrow is shown as an example.*

this stage since there is only a single camera/retina: A higher speed can compensate for a bigger object moving at a larger distance.

By comparing equations 1.5 and 1.6 with equations 1.2 and 1.3 we see that a moving plane generates higher order optic flow terms. This combination of optic flow terms forms one second order flow component called fanning (Kanatani, 1990). One way to generate fanning is by rotating a plane around an axis parallel to the image plane. A pure fanning flow field can be written as in equations 1.7 and 1.8. It can be fully characterized by the parameters F_x and F_y, the fanning in the horizontal (x) and vertical (y) direction, respectively. In Figure 1.5 the direction of the flow represented by F_x and F_y is plotted.

$$u_f(x,y) = F_x x^2 + F_y xy \tag{1.7}$$

$$v_f(x,y) = F_y y^2 + F_x xy \tag{1.8}$$

In chapter 3, the response of neurons in VIP to fanning stimulus will be compared to the response to translation, expansion/contraction, rotation and spiral stimuli

The flow matrices used for generating the optic flow stimuli are the following:

Translation:

$$\begin{pmatrix} u \\ v \end{pmatrix} = \begin{pmatrix} T_x \\ T_y \end{pmatrix} \tag{1.9}$$

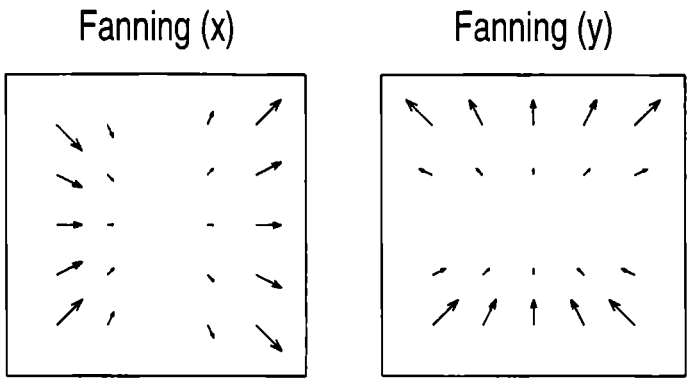


Figure 1.5: *Second order optic flow: Fanning.*

Divergence:

$$\begin{pmatrix} u \\ v \end{pmatrix} = \frac{1}{2} D \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} \tag{1.10}$$

Rotation:

$$\begin{pmatrix} u \\ v \end{pmatrix} = \frac{1}{2} R \begin{pmatrix} 0 & -1 \\ 1 & 0 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} \tag{1.11}$$

Shear:

$$\begin{pmatrix} u \\ v \end{pmatrix} = \frac{1}{2} \begin{pmatrix} S_x & S_y \\ S_y & -S_x \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} \tag{1.12}$$

Fanning:

$$\begin{pmatrix} u \\ v \end{pmatrix} = \begin{pmatrix} F_x x & F_y x \\ F_x y & F_y y \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} \tag{1.13}$$

Here T_x and T_y represent the translation components in the horizontal and vertical direction, respectively. In the same way S_x and S_y describe the shear components in x- and y- direction. Rotation and divergence can each be represented by a single parameter (R and D).

1.3 Visual System

Different properties of the visual scene are analyzed concurrently. The decomposition of the time varying images on the two retinas is done in parallel and to some degree independently of other visual cues. One can distinguish two important tasks for the visual system. One involves orienting in, and movement through, a three dimensional scene, where the input to the central nervous system is coming from two, two dimensional retinas. The second task is the detailed examination, localization and identification of objects, which is associated with the fovea and exploratory eye movements. The

two major projections in the cortex are linked to this "where" and "what" pathway Ungerleider and Mishkin (1982) introduced the idea that extrastriate cortex contains two parallel pathways a dorsal stream leading to posterior parietal cortex ("where") and a ventral stream leading to inferior temporal cortex ("what") The subsequent stations in the "where" processing stage are Retina, Lateral geniculate nucleus (LGN), Area 17 (V1), Area 18 (V2 and V3) and Area 19 (V4 and V5=MT) In figure 1 6 a schematic lateral view of the monkey cerebral cortex is shown (For an overview see Sakata et al , 1997 and DeYoe and van Essen, 1988) At the top level of the hierarchy are the Ventral Intra-Parietal area (VIP), the Medial Superior Temporal area (5a=MST) and the parietal cortex (7a) For a schematic drawing of the interconnections see Fig 1 7 One has to be aware that there are more aspects to stimuli than optic flow, the prime stimulus that will be discussed in this thesis For example, as shown in Fig 1 7, there are disparity and vergence related responses as well In the study presented here, the monkey fixated a red dot on the screen and had both eyes open disparity and vergence were therefore kept constant

There are numerous interconnections between VIP and other visual areas (for a more complete description see DeYoe and van Essen, 1988) Area VIP, the subject of this thesis, is thought to be primarily linked to the "where" pathway However, one can argue that the data presented here, could support the hypotheses that VIP is also involved in "shape from motion" detection, and therefore is involved in the "what" pathway as well, but certainly to a lesser extent In the next section the areas which are most relevant for this study will be discussed shortly Especially MT and MST will receive some extra attention since the visual properties of the neurons in these areas are similar to the ones found in VIP

Retinopy in the visual system

Like in a photo-camera, the outside world is projected upside down on the retina Here, light sensitive rods and cones measure the intensity of a small part of the image An (already) complex intra-retinal process relays the information to the ganglion cells, the output cells for the retina Every ganglion cell responds to a stimulus on a small part of the retina This area, where a change in light condition causes a change in response, is called receptive field (RF) The receptive fields of ganglion cells are composed of concentrically arranged center and surround regions A maximum response is elicited, when the center and surround are stimulated at maximum contrast (light/dark, red/green, blue/yellow) For about half the cells with a center surround organization, stimulating the center increases the response and stimulating the surround decreases it (ON-Cells) For the other 50 percent the opposite is true The center of the RF is antagonistic, while the surround is excitatory (OFF-cells)

Lateral Geniculate Nucleus

The ganglion cells project to the lateral geniculate nucleus (LGN) Neurons in LGN show the same type of receptive fields as the ganglion cells They provide input to the

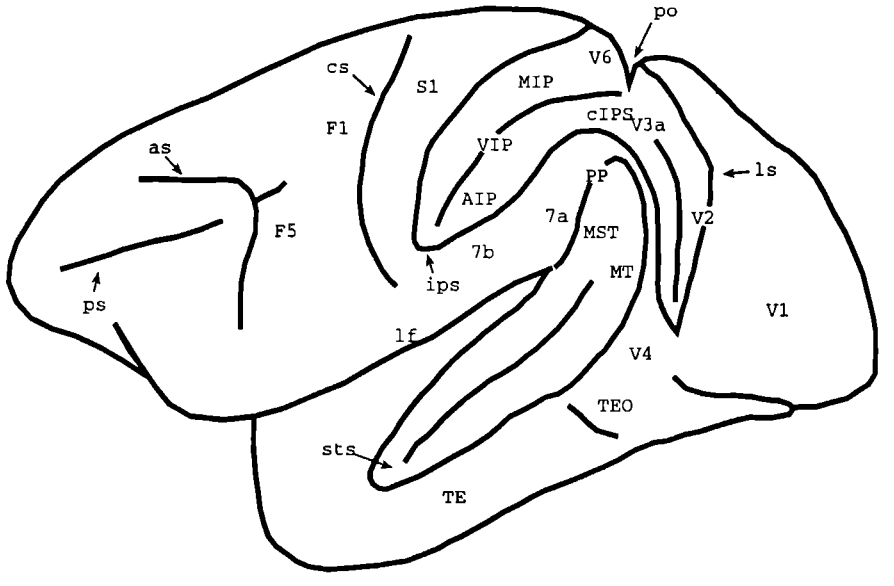


Figure 1.6: *Lateral view of the monkey cerebral cortex (Sakata et al., 1997) showing the inside of the intraparietal sulcus (ips), superior temporal sulcus (sts) and lunate sulcus (ls). The locations of visual areas along the dorsal visual pathways are shown in the diagram. as, arcuate sulcus; cIPS, caudal intraparietal sulcus area; cs, central sulcus; F1, primary motor area; F5, hand region of ventral premotor area; ips, intraparietal sulcus; lf, lateral fissure; LIP, lateral intraparietal area; ls, lunate sulcus; MIP, medial intraparietal area; MST, medial superior temporal area (V5a); MT, middle temporal area (V5); po, parieto-occipital sulcus; PP, posterior parietal area; ps, principal sulcus; sts, superior temporal sulcus; VIP, ventral intraparietal area; V1-6, primary, secondary, third, fourth, fifth and sixth visual areas.*

cortex and regulate the strength of the visual signals. The parvocellular division of LGN contains X-cells, while the magnocellular layers of LGN contain Y-cells. For X-cells, the RF is chromatically as well as spatially opponent. The center and surround parts of the receptive fields are responsive to red (center) and green (surround) light, or visa versa. The center can be excitatory or inhibitory, while the surround is then respectively inhibitory or excitatory. This results in the four basic detector types. A second type of X-cells has a much less pronounced center-surround organization, and the chromatically opponent mechanisms may be coextensive. Their RF responds excitatory to yellow (red and green) and inhibitory to blue or visa versa. Y-cells appear to form a single class. Their RFs have a center surround organization and lack (or show very weak) chromatic opponency. Furthermore, their RFs are in general larger that the RFs of X-cells.

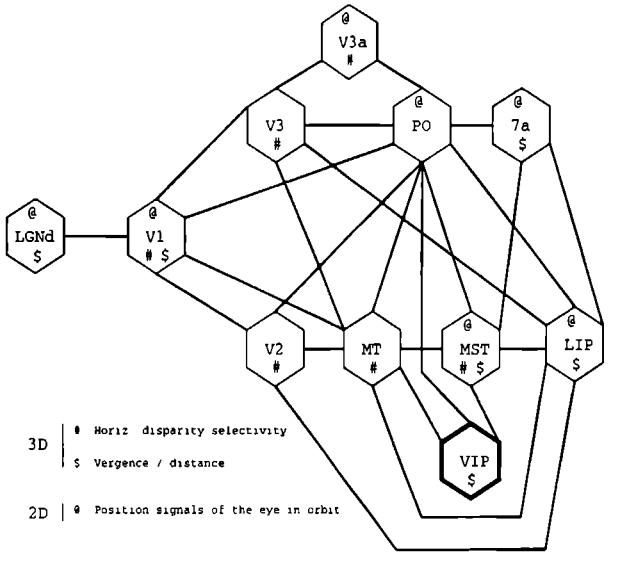


Figure 1.7: *Schematic drawing of the functional circuitry of the dorsal pathway implicated in visual 2-dimensional or 3-dimensional coding (Trotter et al., 1996). The proximity of cortical areas in the scheme does not necessarily represent the anatomic reality, but rather the areas functional interconnections implicated in oculomotor responses. The presence of (#) symbols means that visual activity is present with disparity selectivity, and can be modulated by either the position of the eye in orbit (@) or by viewing distance and/or vergence ($). The absence of these symbols does not mean that the corresponding property does not exist, but rather that it remains to be explored.*

Primary visual cortex (V1)

From LGN, the axons travel via the optic radiation to the cortex. They terminate at the backside of the brain in a part of the cortex situated in the occipital lobes. In this area, the primary visual cortex (V1), many cells are direction selective and most of them are orientation selective. They are responsive to motion in one, and often also in the opposite direction Generally they are also responsive to non-moving bars of the proper size and orientation projected within the receptive field. Hubel and Wiesel (1962) identified two basic cell types in V1 (Area 17, in cat): simple and complex cells. Simple cells have separate ON and OFF zones, enabling them to identify simple elements like bars and contrast gradients. The complex cells form a very heterogeneous group with complex RF properties. In V1 (and LGN as well), the anatomical organization of the cells is retinotopic. This implies that neighboring cells tend to have nearly overlapping receptive fields. Two cells with their receptive fields close together will lie close together in V1 as well, while cells with RFs far apart will be far apart in V1.

Second visual area (V2)

The second visual area (V2) receives its input primarily from V1 Neurons in V2 show pronounced selectivity for binocular disparity, some are chromatically opponent Most neurons in V2 are sensitive to higher velocities compared to V1 The convergence of the 'What' and 'Where' systems seems to be more pronounced in V2 than in V1 Tamura et al (1996) for example, found that in V2 about 21 % of the neurons had a dual selectivity to both color ('What') and direction of stimulus motion ('Where'), versus 5 % in V1

The third visual area (V3)

The third visual area (V3) receives projections from V1 and represents only the lower part of the visual field (Felleman & Van Essen, 1987) Most cells are strongly orientation selective, and many are strongly directionally selective and sensitive to binocular disparity Relatively few are chromatically selective (Felleman & Van Essen, 1987)

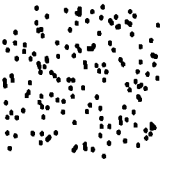
Middle Temporal area (MT)

In area MT, most of the neurons are strongly direction selective (Dubner and Zeki, 1971) MT is relatively insensitive to stimulus form and color (Zeki, 1974, Baker et al, 1981, Maunsell & Van Essen, 1983a, Albright, 1984, Saito et al , 1989) In the foveal part of area MT (RF within 1 deg), some neurons respond also to the tracking of a fixation dot About 83 percent of these foveal MT tracking-neurons are also direction selective (Newsome et al, 1988, Komatsu and Wurtz, 1988, Erickson and Dow, 1989b) The preferred tracking direction is either the same or opposite to the preferred translation direction Furthermore, for 61 % of the neurons the stimulus induced response is modulated by the position of the eyes in orbit (Bremmer et al , 1997b) The pursuit related activity was modulated by eyeposition in 78 % of the neurons tested (Bremmer et al , 1997b)

MT is organized topographically in visual field coordinates (Alleman & Kaas, 1971, Zeki, 1978, Van Essen, 1985) The unidirectional MT neurons show a bias in the distribution of preferred directions (Albright 1989) This bias favors motions falling along radial paths directed away from the center of gaze This bias was significant for eccentricities in the range of 12-30 deg There was no bias found for eccentricities smaller than 12 deg MT receives major direct projections from V1 (Maunsell & van Essen, 1983, Fries, Keizer & Kuypers, 1985) and indirect input via V2 (DeYoe & Van Essen, 1985, Shipp & Zeki, 1985) MT receives also input from V3 (Maunsell & Van Essen, 1983, Ungeleider & Desimone, 1986) About 70 percent of the neurons in area MT showed pronounced sensitivity to horizontal disparity (Maunsell and van Essen, 1983b) Already at the level of MT, 60 % of the neurons show a tuning towards a speed gradient within the stimulus (Treue and Andersen, 1996)

Medial Superior Temporal area (MST)

As in area MT which projects to MST, neurons in area MST are direction selective (Desimone and Ungerleider, 1986) Neurons in MST have larger receptive fields than MT



neurons (Desimone and Ungerleider, 1986, Tanaka et al , 1986) Neurons in area MST respond also with relative selectivity to divergence (contraction/expansion), rotation and combinations of both (spiral stimuli) (Tanaka et al , 1986, Saito et al , 1986, Tanaka and Saito, 1989, Tanaka et al , 1989, Duffy and Wurtz, 1991a, Duffy and Wurtz, 1991b, Orban et al , 1992, Graziano et al , 1994, Lagae et al , 1994) Therefore, it has been proposed that this area plays an important role in motion processing related to movement in a three dimensional environment Most (over 90 percent) of the neurons in area MST are sensitive to disparity of the visual stimulus (Roy et al , 1992) Most (95 percent) of these were most responsive either to near stimuli (stimuli with crossed disparities appearing to movement in front of the fixation point) or to far stimuli (behind fixation point) For a smaller sample the preferred direction reversed for reversed disparity (Roy et al , 1990) For 82 % of the neurons, the stimulus induced response is modulated by the gaze direction of the eyes (Bremmer et al , 1997b) The direction selectivity however, was not influenced by eye position Bremmer et al (1997) further showed that in 80 % of the neurons tested, the pursuit related activity was modulated by eye position

Micro stimulation of clusters of area MST neurons during a two-alternative forced-choice direction simulation task does influence the psychophysical judgments of the monkey in 67 % of the experiments The influence is generally towards the direction of motion encoded by the MST neurons at the stimulation site (Celebrini and Newsome, 1995)

The lateroventral region of the medial superior temporal area (MSTl) is characterized by neurons that respond best to small spots of light A subset of neurons in MSTl shows an integration of direction-specific information from visual, eye (Newsome et al 1988) and head movement related sources (Thier & Erickson, 1992) Therefore these cells may encode target motion in a particular direction by any combination of a directional visual response, a directional eye movement response or a directional response to head rotation Lesions and electrical stimulation of this region appear to modify the maintenance of pursuit eye movements (Dursteler an Wurtz, 1988, Komatsu and Wurtz, 1989) All data suggests that MSTl is primarily involved in signaling the direction of self-motion of the observer through the environment

The dorsomedial region of the medial superior temporal area (MSTd) is characterized by neurons that respond best to large field motion (Komatsu and Wurtz, 1988b) Neurons in MSTd tend to have large RFs, frequently covering more than a full quadrant of the contralateral visual field and extending into the ipsilateral visual field About 90 % of the neurons in MSTd have a preference for the position of the center of first order optic flow (Duffy and Wurtz, 1995) This arrangement creates the potential for graded responses from individual neurons for different directions of heading as an observer moves through the environment In a recent study, Geesaman and Andersen (1996) showed that MSTd is form/cue invariant for complex motions Furthermore, Duffy and Wurtz (1997a) showed that more than 2/3 of the neurons in MSTd are strongly modulated by changes in the mean speed of motion in optic flow stimuli Nine out of ten neurons responded better with than without a speed gradient Many (43 %) of the neurons in MSTd are tuned to the direction of pursuit regardless of the angle of gaze (Squatrito and Maioli, 1997), and about 18 % show a tonic discharge modulated by the static position of the eyes These findings make MSTd an appropriate candidate for analysis of object motion as well as

motion induced by observer translation That heading detection is theoretically possible with MST-like neurons was shown by Lappe et al (1996) using a neural network model to link the response properties of MST-neurons to the psychophysics of human heading detection from optic flow

Area 7a

In area 7a, the large and non-uniform visual receptive fields remain in retinotopic coordinates while the animal changes direction of gaze However, the magnitude of the response to the visual stimulation of the same retinotopic position, is modulated by eye-position (Andersen et al , 1985) Furthermore does area 7a shows saccade related activity (Andersen et al , 1990) A direction-specific pursuit-related activity could be found for 42 % of the neurons in area 7a Furthermore, for the majority of cells, this pursuit related activity was modulated by eye position (Bremmer et al , 1997a)

Area V3a

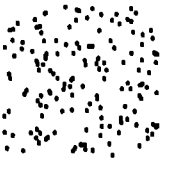
In contrast to area 7a, the receptive fields in area V3a are small and have an uniform profile of excitability As in area 7a, they show a modulation by gaze direction (Galletti and Battaglini, 1989)

The parieto-occipital area (PO or V6)

In the parieto-occipital area, neurons with the same properties as in area V3a and 7a are found (Galletti et al , 1995) About 12 % of the neurons show receptive fields which were organized in spatial instead of retinotopic coordinates (Galletti et al , 1993)

The Ventral Intra-Parietal area (VIP)

VIP, the subject of this thesis, receives visual input from MT (Maunsel & van Essen, 1983a) and MST (Boussaoud et al , 1990, Baizer et al , 1991) The motion-selective area is confined to the floor of the intraparietal sulcus and the adjacent deepest portions of the medial and lateral banks of the sulcus (Duhamel et al, 1991, Colby et al, 1993b) This physiologically well-defined area corresponds to a portion of the MT projection zone Direction and speed tuning are similar to that found in area MT Duhamel et al (1991) and Colby et al (1993b) reported that some VIP neurons are selective for the distance at which the stimulus is presented In addition, some neurons are selective for the anticipated point of contact of a stimulus moving toward the animal, regardless of the absolute direction of visual motion They further reported that the majority of neurons in VIP have somatosensory responses as well Recently Bremmer et al (1996) showed that part of the neurons in area VIP respond to non-retinotopic input In a head fixated monkey, the RFs (on the retina) of these neurons shift with the direction of gaze For some, the RF stayed at the same screen position while changing gaze direction



The latter response pattern suggests a head centered coordinate system for some VIP neurons

The selectivity for direction of a moving stimulus is high in VIP About 80 percent of the neurons respond at least twice as well to a stimulus moving in the preferred direction compared to the null direction (Colby et al , 1993b) The degree of speed tuning is on average twice as broad as that reported for area MT The preferred speed for neurons in VIP ranges from 10 to 320 deg/sec About half of the cells are responsive to smooth pursuit These observations show a large similarity with the observations made in MST In this thesis, data will be presented which was gathered and analyzed in a quantitative way to make a thorough comparison with MST data possible

1.4 Outline of this thesis

Chapter 2: VIP resembles MSTd for optic flow

Chapter 2 will show that the receptive field characteristics of VIP are very similar to those of MSTd neurons It was already known that neurons in the ventral intraparietal area (VIP) respond to translating random dot patterns Such responses can be explained on the basis of the input from the middle temporal area (MT) to this area Anatomical evidence has shown that VIP receives input from the dorsal part of the medial superior temporal area (MSTd) also Neurons in the latter area are thought to be involved in egomotion since they are sensitive to first order optic flow components such as divergence and rotation Because of the MT and MSTd input, neurons in VIP may be expected to show sensitivity to such first order optic flow as well

In this chapter the responses after presentation of random dot patterns exhibiting either expansion, contraction, clockwise or counter clockwise rotation are compared to the responses to translation stimuli tested in eight directions Most VIP neurons showed clear direction selective responses, particularly to expansion but sometimes also to a combination of components (spiral stimuli)

To test whether the scale invariance found in these VIP neurons arose from convergence of translation sensitive sub fields with radial or circular direction preferences ("mosaic hypothesis"), the direction selectivity for translating stimuli was tested over these sub-fields

Chapter 3: Responses in VIP to translation and fanning optic flow

There is evidence that neurons in the medial superior temporal area (MST) respond to rotation in depth of textured planes This chapter presents a study to investigate whether this is the case for VIP as well, since MST neurons project to VIP The movement of a flat board, covered with dots was simulated by a computer The 2-D images corresponded to the projection of structured planes rotating around a fronto-parallel axis In literature this stimulus is called fanning A comparison will be made between the responses of VIP neurons to fanning and the responses to translation, expansion/contraction, rotation and spiral stimuli

Chapter 4: Minimum stimulus duration for optic flow in VIP

The 2-D optic flow projection on our retina contains important information about egomotion A crucial question is how long such optic flow patterns have to be presented to be effective in our decisions about the direction we are moving The detection of optic flow patterns can be achieved despite very short stimulus presentations while fine discrimination tasks often require much longer durations of stimulation This chapter will discuss how well VIP neurons are able to detect optic flow patterns of short duration and discus the neural basis of these perceptual limitations in VIP

Random dot expansion patterns presented for only 2 frames were found to be already effective to elicit responses On average such responses augmented by increasing the duration of the stimulus presentations up to 46 ms for translating stimuli and up to 118 ms for expanding patterns At longer stimulus durations the tonic part of the response became increasingly important (occasionally even showing stronger direction selectivity than the phasic part of the response) It is concluded in this chapter that cells in VIP are well-placed to underlie the ability to detect optic flow patterns of short duration

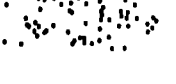
Chapter 5: Rebound properties in VIP neurons

Oscillating visual patterns are frequently encountered in everyday life, especially with respect to egomotion, yet little is known about the responses of cortical neurons to such patterns VIP is a zone in which activity was found to be related to the sensory components of egomotion Because of the responsiveness to for example divergence, one would expect VIP to be responsive during forward and backward body sway (Dijkstra et al , 1994a) Furthermore, the neurons with vestibular input would likely to be active during body sway

This chapter will show that oscillating stimuli can have some surprising effects on VIP neurons The responses to single presentations of optic flow patterns (translation, expansion and contraction) were compared to those obtained when the same stimuli were presented in slow and rapid oscillating movement (0 2 to 6 3 hertz) All neurons tested could be driven by the oscillations and in the majority of the cases the responses were crisper than could have been anticipated on the basis of the presentations of single components of the cycle (constant speed)

Chapter 6: Smooth pursuit in VIP

Retinal optic flow signals have to be combined with extraretinal signals to allow the detection of heading during smooth pursuit When moving forward, one can track objects on the side and thus making a smooth pursuit eyemovement, without loosing sense of the direction in which one is moving This fixation of objects while moving, has several advantages It not only allows a more detailed inspection of these objects but it also provides means for visual stabilization (Miles et al , 1986) For this it is essential that neurons are available which combine information about motion on the retina and about movement of the eye, head and body in space This chapter presents data of VIP neurons tested during pursuit eye movements Evidence will be presented that there is indeed a



convergence of optic flow and smooth pursuit information in VIP, suggesting that there is an overlap between the smooth pursuit class of cells and the population of optic flow coding cells.

Chapter 2

VIP resembles MSTd for optic flow

2.1 Introduction

When an observer moves through a scene or when an object moves relative to an observer, much information can be derived from the time-varying projection on the retina This information can be used to extract the movement of the observer and the motion and shape of objects in the surround Thus, the information derived from optic flow fields has a dual functional role (i) It informs an observer about his self-motion (ii) It informs an observer about the layout of the visual world

In monkey extrastriate cortex, several areas are suspected to be important for the analysis of optic flow Most attention has focused on area MSTd (Tanaka et al , 1986, Saito et al , 1986, Tanaka and Saito, 1989, Tanaka et al , 1989, Duffy and Wurtz, 1991a, Duffy and Wurtz, 1991b, Orban et al , 1992, Graziano et al , 1994, Lagae et al , 1994), which receives input from MT MSTd is the first visual area with neurons tuned to first order basic optic flow components such as those defined by Koenderink and van Doorn (1975), namely curl (rotation, clockwise or counterclockwise), div (divergence, expansion or contraction) and def (deformation, in horizontal or vertical direction) Originally, it was thought that neurons in MSTd could selectively respond to only one of these components, or could perform a decomposition (Saito et al , 1986, Tanaka et al , 1989) However, more recent studies have shown that most neurons in area MSTd are sensitive to several components (Duffy and Wurtz, 1991a, Lagae et al , 1994), or to linear combinations of these components (such as spiral stimuli which are based on a combination

Adapted from S J Schaafsma and J Duysens, Neurons in the ventral intraparietal area of awake macaque monkey closely resemble neurons in the dorsal part of the medial superior temporal area in their responses to optic flow patterns Journal of Neurophysiology Vol 76, No 6, 1996, pages 4056-4068

of divergence and rotation) (Graziano et al , 1990, Orban et al , 1992, Graziano et al , 1994)

In contrast, neurons in MT are mainly responsive to translating stimuli in a direction-selective manner (Maunsell and van Essen, 1983b, Albright, 1984) MT neurons can also respond to more complex optic flow fields than translation, but only when these flow fields contain translation components presented over the RF (Lagae et al , 1994) In further contrast to MST, MT generally lacks "position invariance" for direction selectivity to first order optic flow components

Anatomical studies (Boussaoud et al , 1990, Baizer et al , 1991) have shown that MSTd projects into several areas of the parietal cortex, including area 7a, the superior temporal polysensory area (STP) within the superior temporal sulcus (STS), and VIP Area 7a was found to contain neurons with "opponent vector" sensitivity, well-suited to detect expanding or contracting flow fields (Steinmetz et al , 1987) A similar RF organization was found in STP (Bruce et al , 1986, Hikosaka et al , 1988) In contrast, relatively little is known about the third projection area, VIP VIP receives input both from MT (Maunsell and van Essen, 1983a, Ungerleider and Desimone, 1986, Blatt et al , 1990) and from MSTd (Boussaoud et al , 1990, Baizer et al , 1991)

Previous physiological studies (summarized by Duhamel et al , 1991 and Colby et al , 1993b) have shown that VIP neurons are mostly direction selective and respond well to whole-field translating motion of random-dot patterns On average, they prefer higher speeds and are more broadly tuned for velocity than MT neurons (Colby et al , 1993b) So far, however, translating stimuli have mostly been used to study VIP Also, there have been no systematic studies to explore how VIP neurons react to more complex optic flow patterns as tested by others in MSTd The input from MT and MSTd suggests that neurons in this area might respond to first order optic flow components Moreover, one might expect VIP neurons to exhibit scale invariance, as found in MSTd If so, it would be interesting to explore the mechanisms of such invariance, and to compare the results with those obtained in MSTd For MSTd, one of the models suggested is the vector field hypothesis It is based on the ideas of Koch et al (1982) regarding dendritic processing, and it states that sensitivity to first order optic flow components is a distributed property and could rely on dendritic compartments receiving convergent MT input of neurons with a different direction selectivity (Saito et al , 1986) Alternatively, the direction mosaic hypothesis relies on a "patchwork of planar directional sub-fields arranged to yield large-field aggregate selectivity for planar, circular or radial motion" (Duffy and Wurtz, 1991b)

The present study will address the questions of how optic flow responses of MT and MSTd neurons are represented and transformed in VIP neurons of awake monkeys, and which RF structure underlies these responses

2.2 Methods

The responses of VIP neurons were recorded from two awake male monkeys (Macaca Mulatta both weighing around 6 kg)

Preparation

Surgery was performed under general anesthesia Ketamine (50 mg mixed with 0 25 mg atropine sulfate, intramuscular injection) was used for the initial anesthesia Halothane with a mixture of N_2O and 32% O_2 was applied during the rest of the surgery During the first operation a skull cap was installed using titanium bone screws and dental cement (Resin Kaltpolymerisat, Paladur©) This cap, which contained four bolts embedded in the cement, allowed for rigid fixation of the monkey's head during experiments In a subsequent operation, a polished copper ring, plated with gold, was implanted on the monkeys right eye for the recording of eye-movements (Judge et al , 1980) The monkeys were then trained to perform accurately on a fixating task, using water as a reward After training was completed, a trephine hole of 16 mm diameter was made during a third operation A stainless steel chamber was mounted on the skull over the parietal cortex A second chamber was placed on one of the animals to be able to record from the second hemisphere

Stimuli

For quantitative tests, stimuli were generated by a graphics workstation (HP-9000/433S-TVRX-T1) at a 60 Hz frame rate The awake monkey was sitting in front of a 2 x 2 5 meter translucent screen, situated at a distance of 46 0 cm The viewing area of the monkey was 117° x 113° This viewing area was larger than the one used in most other studies on MSTd and VIP Nevertheless the viewing area still did not completely coincide with the complete physiological viewing range of the monkey Hence it could be that a few of the most peripheral receptive fields were not stimulated over the entire receptive field For the majority of neurons, however, the viewing area was adequate to allow stimulation over the full extent of the RF All stimuli were calculated on-line and projected on the screen by a Barco graphics 400 video projector Experiments were conducted under scotopic background conditions (0 05 Cd/m^2) The stimuli were green (phosphor p53) and had a luminance of 0 5 Cd/m^2 The software allowed for stimulation with optic flow patterns (up to second order) in any position within the viewing window For translation stimuli, all dots moved in the same direction (8 directions used) For divergence stimuli, all dots moved towards the center (contraction) or away from it (expansion) For rotation stimuli, all dots moved clockwise or counterclockwise at the same distance from the center The spiral stimuli were constructed with combinations (2x2) of the divergence and rotation stimuli, so that all dots moved clockwise or counterclockwise around, and at the same time moved away or towards the center

The stimulus normally consisted of 40 dots, except for a few experiments in which the effects of masking was studied (masking parts of the stimulus area) To keep the ratio of stimulated over non-stimulated areas constant, the size of the dots depended on the size of the stimulated area when all 40 dots were shown Some preliminary experiments (7 neurons) showed that dot size and density were relative unimportant for the neurons in VIP This relatively unimportance of the dot size is similar to MSTd, where Tanaka and Saito (1989) showed that changes in these parameters were of little importance in

determining the response levels Because of these initial trials, an arbitrary dot size of 4 7° was chosen when the stimulus was projected on the complete screen (117° x 113°) With 40 dots, this results in a 21 density factor (fraction of area covered with dots) Since there were relatively few dots, it was felt that such large dots were sometimes needed to activate the neurons optimally For a smaller stimulus area, for example 12° x 11°, the diameter of the dots was 0 5° At the lower end, the size of the dots was limited by the pixel size (0 1° diameter) In the summation test, when only a part of the stimulus was shown, the stimulus was not scaled down to the visible stimulus area In this test, the stimuli over the subsections had the properties (speed, dot size, etc) of the complete, unmasked stimulus

The standard lifetime of each dot was 332 msec (except for some preliminary experiments when it was 133 msec) For six neurons, the influence of the dot lifetime was tested qualitatively On the basis of these tests a value of 20 frames (332 msec) was chosen for all the subsequent experiments Shorter lifetimes resulted in a reduced response for some neurons Longer lifetimes induced a stronger density cue and was therefore less desirable In each stimulus, the mean dot speed was constant (66 7 or 100°/s) Although these speeds were relatively high, they were found to elicit strong responses in VIP For translation, dot speed was the same everywhere For the first order flow fields, it varied from zero in the center, to twice the mean dot speed at the border of the stimulus Note that these speeds are fast relative to the speeds used to study other visual areas Most studies in MSTd used an average speed of 40°/s (Tanaka and Saito, 1989, Duffy and Wurtz, 1991a, Duffy and Wurtz, 1995) Colby et al (1993b) reported a distribution of preferred speeds ranging from 10 to 320°/s for VIP They reported that the degree of speed tuning was on average twice as broad as reported for area MT Optimum speeds reported for MT ranged from 2 to 256°/s (Maunsell and van Essen, 1983b), 5 to 150°/s (Rodman and Albright, 1987) and 2 to 90°/s (Lagae et al , 1994)

A red dot (0 64° diameter) was used as a fixation point The fixation dot could be made to move in a circle to test if the neuron was involved in smooth pursuit

Experimental paradigm

Prior to the experiment (18 hours), the monkey was deprived of water During the experiment the calibration of eye position was tested at regular intervals For this purpose, the monkey had to make saccadic eye movements to 9 different positions which he then had to fixate (using a red fixation dot) for a duration of 3 seconds After correct fixation the monkey was rewarded with water During the quantitative trials, the monkey was rewarded for correct fixation within an electronic window (4° x 4°) This window was kept relatively large to keep the monkey cooperating Trials with poor fixation could be eliminated at a later stage Saccade related activity was evaluated by recording the neural activity during spontaneous eye movements in the rest periods At the end of each session the monkey could drink at libitum

After the isolation of a single unit, the responses of the neuron and the location of the RF were first tested qualitatively with a hand-held projector With this projector, a light bar or a random dot pattern could be shown, and the neurons could be tested for their

sensitivity to translation, rotation and divergence This generally allowed for a rough determination of the optimal type of stimulation, and both the size and location of the RF For quantitative testing, the stimuli were generated by the HP stimulus computer while the monkey fixated Trials lasted mostly for 15 seconds During these fixation periods first the background activity was sampled for one second Secondly, one up to five stimuli were shown The pause between subsequent stimulus presentations was 1 5 seconds The different fixation periods were separated by 5 up to 10 seconds

If the response showed signs of adaptation, the fixation periods were shortened Only one stimulus was then shown for each fixation period (lasting 3 s) and pauses of 10 seconds were used During quantitative testing, the stimuli were first used to determine the location of the RF The on-line construction of the optic flow patterns allowed for a flexible optimization of the stimuli for each neuron By repeating the same stimulus at slightly different locations and with different sizes, a good determination of the optimal location and size of the RF could be made After the definition of the RF, the responses to translation in 8 different directions was tested Subsequently, the neurons were tested for rotation, divergence and combinations of these two (spirals) All stimuli were shown in pseudo random order during the fixation periods All types of stimuli within an experiment were given with equal frequencies The number of repetitions for each experiment ranged from six to fifteen times, but occasionally up to forty trials were sampled The number of repetitions was based on the on-line build-up of the response histograms for every stimulus All neurons were tested binocularly

Recording

Recording sessions were usually conducted twice a week Typically, about two neurons could be studied in detail during one session During the experimental sessions, the recording chamber was filled with NaCl 0 9 % to prevent cortical pulsations and thus ensuring stable recordings Neurons were recorded with home-made glass-coated tungsten electrodes ($0\,6 - 1\,5 M\Omega$ at 1 kHz) When more than one unit was recorded simultaneously, the action potentials were discriminated routinely using two level detectors If there still was doubt about the spike separation, a custom-made spike analyzer was used as described elsewhere (Epping, 1985) When multi-unit recordings were made, only the most reliably separated unit was chosen for further analysis

With a gold-plated copper ring in the eye (see preparation), a signal related to the eye position was obtained using the double magnetic induction method (modified search coil technique, Bour et al , 1984) Eye movements were recorded at 100 Hz In addition to the eye position signal, the time of occurrence of action potentials, the reward, the vertical retrace of the video signal and the blue line of the video output was recorded The vertical retrace corresponded to the exact onset of every frame in the stimulus The blue line made it possible to align the onset and offset of the stimulus with the neuronal responses and the eye movements In Fig 2 1 the onset and offset of the stimulus are shown as a vertical line All data (eye position signals, action potentials, video timing signals, reward timing) were collected by a special purpose hardware interface composed of several 12 bit analog to digital converters and timers (time resolution 10 micro seconds)

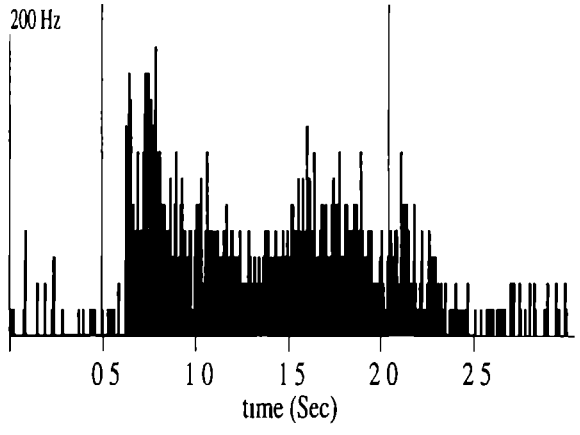


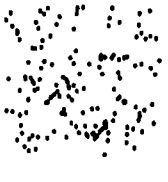
Figure 2 1 *Average (N=7) responses to an expansion stimulus of VIP neuron D3 1 The bin size was 8 msec The onset and offset of the stimulus is indicated by the two solid lines at 0 5 and 2 1 seconds*

Off-line analysis

All trials during which the fixation was insufficient were rejected In most of the rejected trials, the monkey presumably fixated one of the moving dots, or was not fixating at the onset of the random dot stimulus The selected responses to the repeated stimuli were averaged and PSTHs (peri-stimulus time histograms) were constructed An example of an averaged response of a VIP neuron responding to expansion, is shown in Fig 2 1 There was a clear phasic ON response followed by a tonic discharge Latency was typically about 80-100 msec

Several response characteristics were calculated from this histogram The amplitude of the responses was evaluated by measuring the maximum firing rate (MFR, highest spike count in a single bin) and the average firing rate (AFR) The calculation was done for the period between the on- and off-set marker Both measures gave comparable results, but, in this chapter, all data are represented as AFR because many neurons showed both a phasic and a tonic response and MFR does not represent tonic components well The latency of the responses was based on a comparison between the response and the background activity in the 500 ms period prior to the onset of stimulation The point at which the response first crossed a level corresponding to four times the standard deviation of the background activity was taken as the latency

To determine the optimal direction and the tuning width of the neurons for translation, eight different directions were tested The responses were plotted in a polar plot and then fitted (Levenberg Marquardt nonlinear regression, Press et al , 1992) A simple cosine profile (response $R(\phi) = b + k\,cos(\phi - \phi_0)$, where b, k and ϕ_0 are the fit parameters) could not be used for sharply tuned neurons Hence, a Batschelet distribution



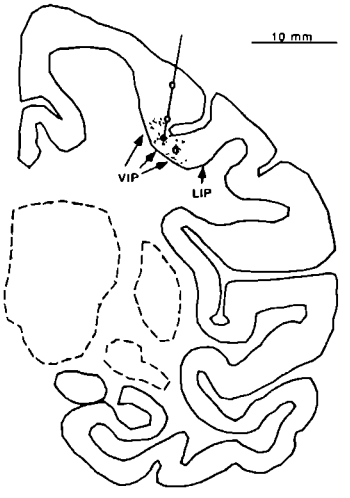


Figure 2.2: *Section in the coronal plane (9.1 mm anterior) with tract reconstruction guided by four lesions. The four lesions are indicated by circles. Three lesions were positioned inside VIP. One lesion was made well outside VIP to get a good direction estimate of the direction of the tracts. VIP is indicated by the dotted area as based on the integrated estimate using both physiological and histological data from the present and previous studies.*

(Batschelet, 1981) was used. For further details : see results (direction tuning).

Histology and reconstruction

At the end of the series of recording experiments the first monkey was sacrificed with an overdose of sodium pentobarbital. Formaldehyde 10 % was used to perfuse the brain, which was later put in a sucrose solution. Serial sections of 40 microns were made in the coronal plane to allow tract reconstruction. Alternating sections were treated with cresyl violet for cell body staining and with Giemsa method for myelin staining.

Reconstruction of the tracts was based on multiple electrolytic microlesions as illustrated in Fig. 2.2. These lesions were made at the end of experiments in both hemispheres, one week prior to perfusion. The electrode coordinates in the second monkey were similar to the ones used for the first monkey. Moreover, the physiological characteristics (visual and somatosensory responsiveness) were the same, thus the 8 neurons from this third hemisphere could be classified as belonging to VIP.

Evaluation of direction tuning

The responses of the quantitatively measured VIP neurons were plotted in polar plots and then fitted (Levenberg-Marquardt nonlinear regression, Press et al , 1992) The definition of the fitted Batschelet profile (Fig 2 3) is response $R(\phi) = b\,exp(k\,cos(\phi - \phi_0 + \nu\,sin(\phi - \phi_0)))$ Here b, k, ν and ϕ_0 are the fit parameters and ϕ the direction of the flow in polar coordinates This function can be regarded as a generalization of the gaussian to circular statistics The tuning direction (ϕ_0), the tuning width (TW) and the fitted maximum response ($FMR = R(\phi_0)$) are a more convenient set of parameters to describe the fitted curve The tuning width ($TW^2 = \left(\int_0^{2\pi} cos(2\phi)R(\phi)d\phi\right)^2 + \left(\int_0^{2\pi} sin(2\phi)R(\phi)d\phi\right)^2$) represents the broadness of the tuning curve in the same manner as the sigma represents the width of a gaussian Since the tuning direction was measured in relatively crude steps (45°), the use of this fitting procedure improved considerably the estimate of the preferred direction and the broadness of tuning

To calculate the significance of a fit, the F-test (Judd and McClelland, 1989) was used This test compares the reduction in variance brought about by the model (the Batschelet distribution) with the average reduction expected from a random set of numbers One can think of this numerator F as the average proportional reduction in error per parameter added, divided by the average proportional reduction in error that could be obtained by adding all the remaining parameters For the Batschelet distribution to be significantly better than the mean response model (this means no tuning), one wants the average error reduction for the parameters added to be greater than the average error reduction we could get by adding the remains of the possible parameters Hence if F is about 1, we are doing no better than one could expect on average So a value of F near 1 suggest there is no tuning in the response Furthermore the significance of the fit (p) was calculated

The criterion used for direction selectivity was based on the fit with the Batschelet distribution All fits with an F > 1 5 were accepted as following the Batschelet distribution and being direction selective Note that if the fit parameter k would not be significantly different from zero, the tuning curve could be simplified to $R(\phi) = b$ F would approach 1, since the parameters ν and ϕ_0 would not contribute much to improve the fit Fitting a tuning curve is a stronger criterion for direction selectivity than the test based on the direction index (DI) calculated from the responses in the preferred and non-preferred direction (Rodman and Albright, 1987) The criterion presented here, rejects neurons where the direction index was bigger than 2 if the tuning was very noisy This is optimal when more than two directions are tested since it takes all data points into account and not just the two nearest to the preferred and non-preferred direction The standard deviation was calculated for the fitted parameters (b, k, ν and ϕ_0) For ϕ_0 this standard deviation indicates how precise the tuning is measured Note that this measure is not the same as F, which states how well the data follows the Batschelet distribution

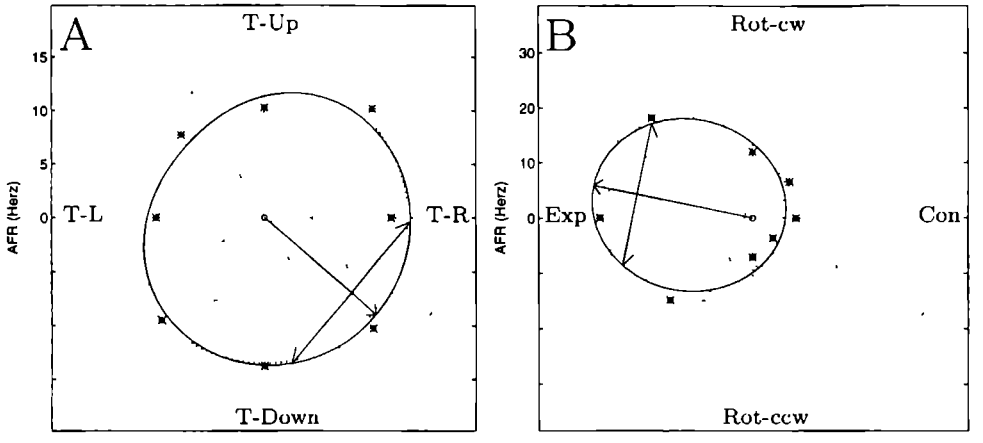


Figure 2.3: *Two examples of a tuning curve fitted through eight data points. The direction of the flow is represented by the angle (ϕ) in this polar plot. Directions of 0, 90, 180 and 270 degrees in graph A refer to preference for translation in the rightward (T-R), upward (T-Up), leftward (T-L), downward (T-Down) directions, respectively. The tuning for divergence and rotation is also plotted in a polar manner. Directions of 0, 90, 180 and 270 degrees in this case refer to preference for contraction (Con), clockwise rotation (Rot-cw), expansion (Exp) and anti-clockwise rotation (Rot-ccw) respectively. Intermediate angels correspond to a mixture of two of these orthogonal flow components. The distance to the center represents the AFR which scale is shown on the side of the plot. We fitted the response curve by a Batschelet distribution with the direction tuning (ϕ_0), the tuning width (TW) and the fitted maximum response (FMR) as characterizing parameters. The values for curve A are* $\phi_0 = -40.5° \pm 18.8°$, $FMR = 13.8 \pm 0.9$ *Hz and* $TW = 77.9° \pm 1.3°$, *where F=1.8 and p=0.32. The fitted values for curve B are* $\phi_0 = 168.4° \pm 5.7°$, $FMR = 29.3 \pm 2.0$ *Hz and* $TW = 63.5° \pm 2.9°$. *Where F=20.2 and p=0.017. The preferred direction is indicated by the two arrows emerging from the center. Perpendicular to this the tuning width (TW) is shown.*

2.3 Results

This chapter is based on a group of 52 neurons which could be measured long enough to obtain quantitative tests with several types of translation (33 neurons) and/or first order optic flow (41 neurons) stimuli and could be fitted by a Batschelet curve. A total of 106 neurons gave significant responses to a moving light bar or a random dot flow field. They are a subset from a group of 178 qualitatively identified neurons in the intraparietal cortex. Tabel 2.1 provides an overview. These neurons could be classified on the basis of histology as belonging to either LIP or VIP. The LIP sample consisted of a total of six neurons which responded only in relation to saccades. All were located anterior to the main sample, at depths between 3.5 and 12.2 mm. The remaining neurons

belonged to VIP. The main emphasis of the present investigation was on visual responses. Nevertheless, it was often possible to investigate the responses to other modalities as well. A total of 33 VIP neurons responded to smooth pursuit eye movements (see further in chapter 6). The neurons were not tested systematically for somatosensory responses. Nevertheless, two neurons were found which responded only during tongue protrusion, but were not visually driven. Their responses correlated with the monkey's drinking liquid reward Another neuron was only responsive upon touching the monkeys face. The three identified somatosensory neurons (found in two hemispheres) were all within the posterior region of the sample, at a depth of 4 to 5 mm Of the remaining neurons, there were 3 which were only responsive to the onset of the presentation of a fixation dot. These neurons resembled MTf (foveal MT) neurons with very small receptive fields as described by others (Komatsu and Wurtz, 1988b; Newsome et al., 1988). Another 4 neurons were responsive only to the onset of the presentation of a large dot pattern.

Area	Number of neurons	Responses to
LIP	6	Saccades
VIP	23	Smooth pursuit only
VIP	3	Somatosensory
VIP	4	"ON" response only
VIP	3	Small slit (resemble foveal MT)
VIP	33	Unclassified
VIP	10	Smooth pursuit and moving visual stimuli
VIP	96	Moving light bar / dot pattern
total·	178	

Tabel 2.1

Figure 2 4: *Summary of responses of VIP neurons to translation (top; 8 directions) and to first order optic flow components (bottom). On the left side the tuning for translation, divergence and rotation is plotted in a polar manner. Directions of 0, 90, 180 and 270 degrees in graph A refer to preference for translation in the rightward (T-R), upward (T-Up), leftward (T-L), downward (T-Down) directions, respectively. For divergence and rotation directions of 0, 90, 180 and 270 degrees refer to preference for contraction (Con), clockwise rotation (Rot-cw), expansion (Exp) and anti-clockwise rotation (Rot-ccw) respectively. The distance to center represents the log of the inverse standard deviation (scaling indicated for 3 values). Thus, points far from the center represents tuning curves with a high precision (best standard deviation was 1.0 degrees, worst SD was 41 degrees) Stars represent data fitted with a Batschelet profile (based on 8 conditions); circles represent data fitted with a cosine profile (based on 4 conditions). On the right, graphs compare the tuning for translation (top) or divergence and rotation (bottom) with the broadness of the tuning. The x-axes scale is in degrees to conform to the labels used in graph A and C and the format of Fig. 2.3. Standard deviations are shown as lines. The arrow indicates the same neuron as shown in Fig. 2.3.*

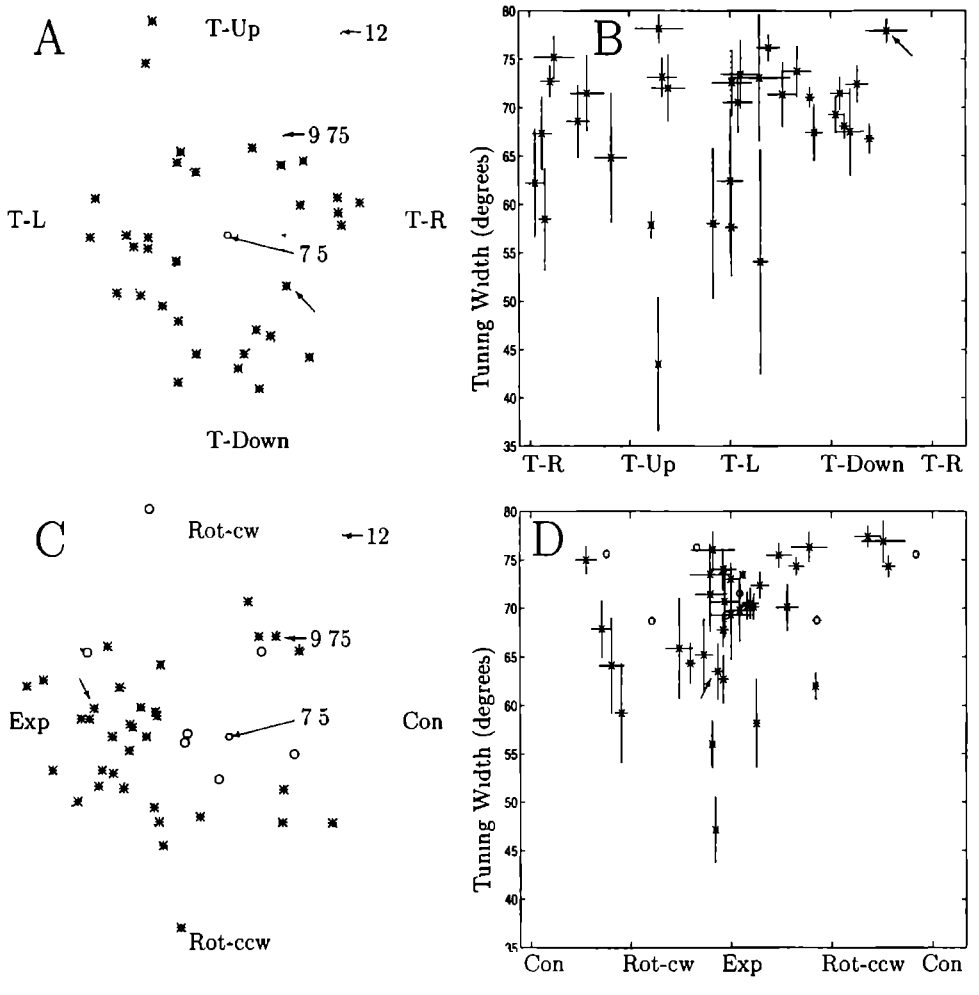


Figure 2 4

Quantitative testing

Generally speaking, the quantitative analysis mostly complemented the qualitative analysis However, for neurons with large receptive fields, the size of the RF was almost invariably larger in the quantitative test (computer) than the estimate based on the qualitative stimulation (hand-held projector)

In the group of quantitatively tested neurons, significant tuning plots (as illustrated

in Fig 2 3) were obtained for 33 neurons tested for responses to translation in 8 directions (Fig 2 4, Top) and for 41 neurons tested for responses to first order optic flow components (Fig 2 4, Bottom)

For the group of 33 neurons tested for translation, all data could be represented well by a Batschelet curve They showed a clear tuning in one direction (mean F of 17) In Fig 2 4 these neurons are represented by stars

Among the group of 41 neurons tested for responses to first order optic flow and fitted by a tuning curve, a total of 7 (circles) were tested with 4 "directions" (expansion, contraction, clockwise and anti-clockwise rotation), while the remaining 34 neurons (stars) were also tested with a mixture of these components (4 "spiral" directions) Of the 7 neurons tested in 4 optic flow "directions" only, all could be fitted well by a cosine profile but not by a Batschelet profile Another 6 neurons, excluded from this sample, yielded a fit with an F below 1 5, and showed no direction selectivity Fitting these neurons with a cosine profile (more sensitive to a broad tuning) confirmed this result

Note that directions of 0, 90, 180 and 270 degrees in Fig 2 4C and D refer to preference for contraction, clockwise rotation, expansion, and anti-clockwise rotation respectively In addition, most of these "divergence" neurons showed more reliable responses to expanding stimuli than to translating ones (the distance from the center is the inverse of the standard deviation of the responses, compare Fig 2 4A and C) This illustrates that these neurons are more specialized for expansion than for translation On the other hand, such specialization often was not very pronounced, since the tuning width for first order optic flow was broad for most neurons (Fig 2 4D) The data point belonging to the neuron illustrated in Fig 2 3 is indicated by a separate arrow

A total of 22 neurons were tested both with translation and first order optic flow stimuli In Fig 2 5 the responses to these 2 types of stimuli are compared There was no correlation between direction preference (translation) and preference for first order optic flow (Fig 2 5A) When tuning width was compared (Fig 2 5B) it was evident that most neurons showed a broad tuning for both types of stimulation

Divergence neurons

There were no true single component neurons found in VIP However, there was a clear bias towards sensitivity for expansion To illustrate the RF characteristics of this group of expansion sensitive neurons (20 neurons with largest responses for expansion when tested with first order optic flow patterns), two will be described in detail One of these neurons was a typical pursuit neuron, the other had no oculomotor related activity

The first example (neuron J7 5, Fig 2 6) responded during smooth pursuit to the lower right of a small target in darkness When tested during fixation, the neuron responded to moving random dot stimuli presented over the whole visual field As found for other neurons in the "divergence" group, the neuron had a large RF (64° x 62°)

When tested with translating random dots over the whole field the neuron responded optimally to movement to the right (Fig 2 6A) Stimulation with expanding optic flow patterns yielded responses as well, but there was no response related to rotating or contracting flow fields Hence, this neuron would fit into the category of double component

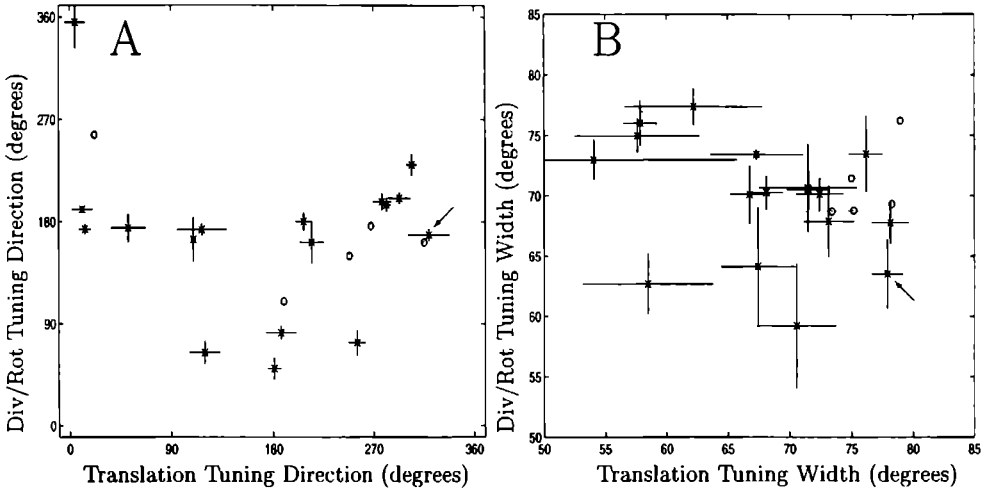


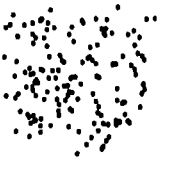
Figure 2.5: *Comparison of responses to translation versus divergence/rotation. In graph A the preferred direction for translation is plotted against the tuning for divergence and rotation. Stars represent data fitted with a Batschelet profile. Circles represent data fitted with a cosine profile. Graph B compares the width of the tuning for direction of translation with the tuning width for divergence and rotation. Standard deviations are shown as lines. The arrow indicates the same neuron as shown in Fig. 2.3.*

plano-radial neurons as described by Duffy and Wurtz (1991a). However, some combinations of divergence and rotation ("spiral stimuli"; Graziano et al, 1990, 1994) evoked responses as well (Fig. 2.6B).

Responses to stimulation of RF subsections

To test the fine structure of the RF, the effective area of stimulation was subdivided in 9 sections, and the same translating stimulus was shown over each subsection. The result of this test is shown in Fig. 2.7A. It can be seen in Fig. 2.7A that each of the 9 subsections of the RF still responded when stimulated in isolation. However, the responses were smaller than for whole field stimulation. As was usually found, the RF was most sensitive in the central region. The RF was least sensitive in the upper contralateral (left in figure) corner. Of all translation responsive neurons, a total of 24 neurons were tested in the way illustrated in Fig. 2.7A. In all cases it was found that the smaller translation stimuli were effective in driving the neurons. For some sub-regions the responses were relatively small. This could indicate that such stimuli covered only part of the RF under such circumstances. There is indeed no reason to assume that the size of the RF fitted exactly the rectangular form of the stimulus area (see also Lagae et al. for MSTd).

The scale invariance was also tested for the preferred stimulus for other optic flow



patterns such as divergence and rotation. To test scale invariance for divergence, the expansion pattern used in Fig. 2.6 was scaled down and presented over 9 sub-regions of the RF (Fig. 2.7B). Responses were found in 6 out of the 9 sub-regions; sensitivity was highest for the middle row.

A total of 27 neurons were examined with this type of test illustrated in Fig. 2.7B. In all cases the response to the preferred stimulus over the whole RF was not significantly different from the response to the preferred stimulus scaled down to the subsections. This is illustrated in Fig. 2.8A in which the ratio of best subsection response over whole field response is plotted. Note that the mean ratio (.93) was only slightly below 1, indicating that overall the best subsection response was barely inferior to the whole field response. However, if all sub-fields are taken into account the situation is different. In Fig. 2.8B the mean ratio for all the sub-fields versus whole fields tested is shown (for each neuron a mean ratio was calculated on the basis of all sub-fields). The mean ratio for the whole population was .64, which was substantially lower than the mean ratio for

Figure 2.6: *Responses of a VIP neuron (J7.5) to translation (A) and various first order optic flow components (B). In the right lower corner in each figure the size of the stimulus area is shown. The outer border represents the field of view of the monkey (117° x 113°). The inner square (with the diagonal lines) corresponds to the area stimulated (64° x 62°). The small circle indicates the position of the fixation dot (middle of the screen). The data in this figure are plotted in a polar manner. The center corresponds to zero activity. The radial axis corresponds to the AFR. The angular dimension represents the stimulus parameter (direction of translation in A). For graph B there are divergence, rotation and a linear combination of these principal flow components. As in the plot for translation (A), a 90 degrees angle in this plot means that both stimuli are orthogonal to each other The solid line connects the AFR as measured during the whole stimulation period. The dashed line represents the mean background activity during half a second before stimulus onset. The error bars indicate the standard deviation. The data points were simply connected to each other to obtain the summary plot. If instead the data are fitted with a Batschelet distribution, the values for the translation curve (A) are* $\phi_0 = 13.5° \pm 5.8°$, $FMR = 66.3 \pm 6.5$ *Hz and* $TW = 58.5° \pm 5.4°$. *Where F=12.2 and p=.034 The values for the first order optic flow components curve (B) are* $\phi_0 = 173.3° \pm 4.6°$, $FMR = 50.0 \pm 2.6$ *Hz and* $TW = 62.7° \pm 2.5°$. *Where F=23.1 and p=.014. Due to poor fixations in the translation test of this experiment, 60 percent of the trials was rejected for the stimulation in the PD. Furthermore this cell showed a large variation in background (zero up to sixteen spikes in the first 0.5 sec before stimulus onset). This resulted in a poor estimate (large SD) of the background response for some translation directions. Note that the response suffers less from the small number of trials, as indicated by its standard deviation. Application of a less rigorous selection criterion was unacceptable since this cell was responsive to eye movements. Accepting more trials (with poor fixation) would have resulted in a less precise response estimate (higher SD's and higher p value for fit).*

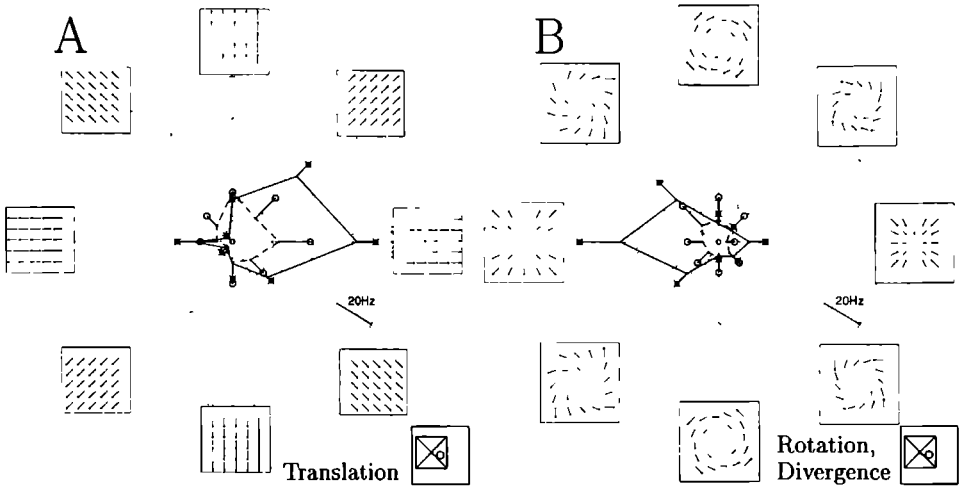


Figure 2.6

the best responses (compare Fig. 2.8A and B). Note that if the nine sub-fields were equal and if the whole RF had a homogeneous structure, both histograms would have looked the same.

Test of direction mosaic hypothesis.

From the direction mosaic hypothesis one would expect that testing a divergence responsive neuron with smaller translation stimuli over parts of the RF, would result in a tuning curve with the direction of translation following the flow in the divergence. For example, testing the right upper corner of the RF of an expansion sensitive neuron with translation in various directions would yield larger responses for translation in the direction of the right upper corner than for other directions. For the VIP neuron, such as shown in Fig. 2.9 this was clearly not the case.

Most tuning curves for the smaller translation stimuli in Fig. 2.9, had the same direction preference as for translation over the whole RF (preference for movement to the right). This result is in conflict with the mosaic hypothesis. In total, 5 neurons were tested completely with this time-consuming method of small translating stimuli in a 3x3 grid, moving in 8 different directions. In none of these neurons was there evidence of a radial arrangements of sub-fields.

A second approach to investigate the RF organization consisted in masking parts of the RF (see also Duysens et al., 1985). This method was especially attractive for neurons with weak tuning for direction of translation (neurons inappropriate for exploring the variations in direction selectivity in sub-fields of the RF). An example of such a neuron

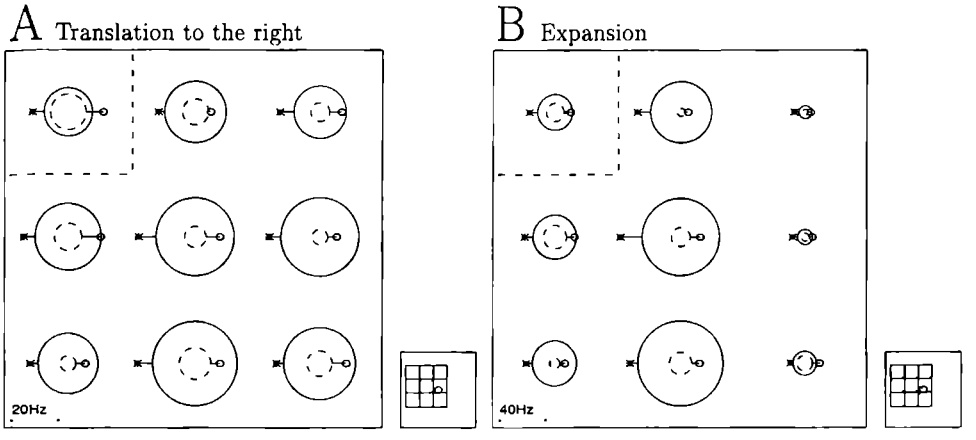


Figure 2.7: *Schematic presentation of the averaged responses to translation (A) and expansion (B) stimuli presented over one of nine subsections of the RF of neuron J7.5. The stimuli were shown in a 3x3 grid of size 21° x 21° each, as indicated by the nine squares in the RF. The radius of the solid lined circle corresponds to the averaged level of activity (AFR) during responses. The dashed line represents the mean background activity during half a second before stimulus onset. The error bars indicate the standard deviation. For the left graph, translation to the right was tested (preferred direction) and the size of the dots was not scaled down (compared to stimulation of the complete RF). For graph B, the stimulation area was the same as in graph A. Expansion patterns were used which were scaled down proportionally to the stimulation area.*

is given in Fig. 2.10. This neuron was sensitive to first order optic flow components but with no eye movement related responses.

The neuron shown in Fig. 2.10, responded vigorously to various types of moving stimuli such as a light bar or noise patterns. When full field translating dot fields were used, the neuron lacked a strong tuning for direction (Fig. 2.3A and Fig. 2.10A). When tested with rotating and diverging patterns over the full field, the neuron showed a distinct preference for expansion (Fig. 2.10B). Some spiral stimuli, constructed by a combination of rotation and expansion, were also quite effective. Contracting stimuli failed to yield either facilitatory or suppressive responses (actually only one neuron showed inhibition while stimulated with the non-preferred first order optic flow stimulus). Before starting the masking test, the neuron was first tested for scale invariance and for optimum stimulus size.

To test for scale invariance, the same neuron was presented with a scaled-down expansion stimulus over 9 subsections of the RF. As seen in Fig. 2.11A, most of the sub-fields yielded responses to (scaled-down) expanding flow fields. Note that significant responses to expansion were obtained in 8 of the 9 sectors investigated. The presence of responses to expanding stimuli, shown in various divisions of the full field, excludes the possibility

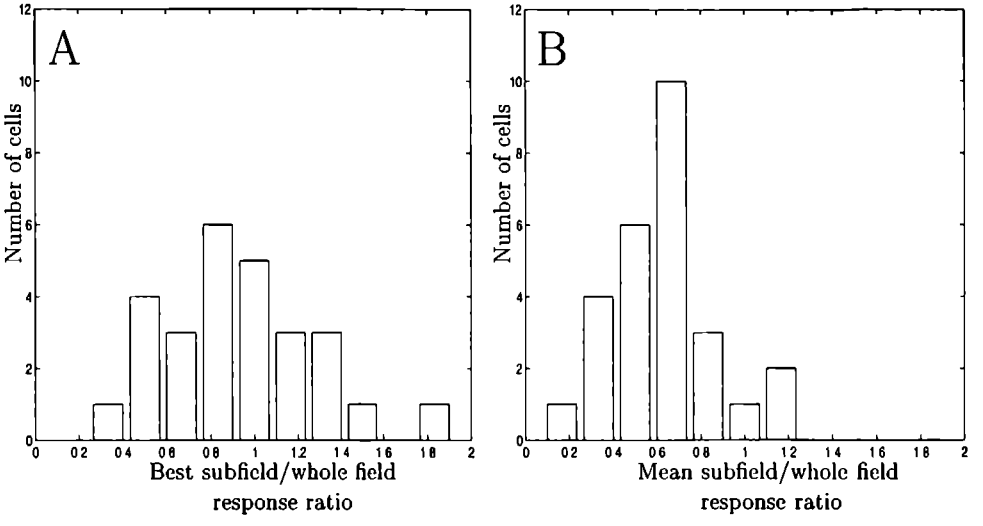


Figure 2.8: *Response ratios of sub-field stimulation relative to whole field stimulation for first order optic flow (N=27). The distribution of the relative response to stimulation of the best responding sub-field is shown in graph A. Its mean is 93 percent. In graph B, the distribution of the mean sub-field response is shown relative to whole field stimulation. Its mean is 64 percent. The sub-field areas were* $1/9^{th}$ *the size of the whole field, as shown in Fig. 2.7B.*

that the sensitivity to divergence of the whole field was generated through accidental activation of a small translation sensitive sub-field, as was observed in MT neurons ("elementary optic flow component sensitivity induced from a translation-selective RF"; Lagae et al., 1994). Furthermore, tests such as illustrated in Fig. 2.11 showed that the RFs were not homogeneous, as was also observed by others for MSTd neurons (Lagae et al., 1994; Duffy and Wurtz, 1991b).

By testing several sub-field sizes, it was found that optimal responses were obtained for stimulation over the right bottom quadrant of the RF (Fig. 2.11B; note the difference in scale with Fig. 2.10B). The broadness and direction of the tuning curve were not significantly ($p>0.95$) different from the ones for the whole field stimulation (Fig. 2.10B), but the responses were twice as large as for stimuli presented over the full field.

After having carefully determined the most effective area for stimulation (both qualitatively and quantitatively: see Fig. 2.10,2.11), a series of tests with masking was performed. The aim of these tests was to investigate how important spatial summation was for these neurons and whether central and peripheral parts of the RF were equally effective. To explore these questions, only a part of the stimulus was shown (hence, in this case, the stimulus was not scaled down but there was simply a reduction in stimulated area).

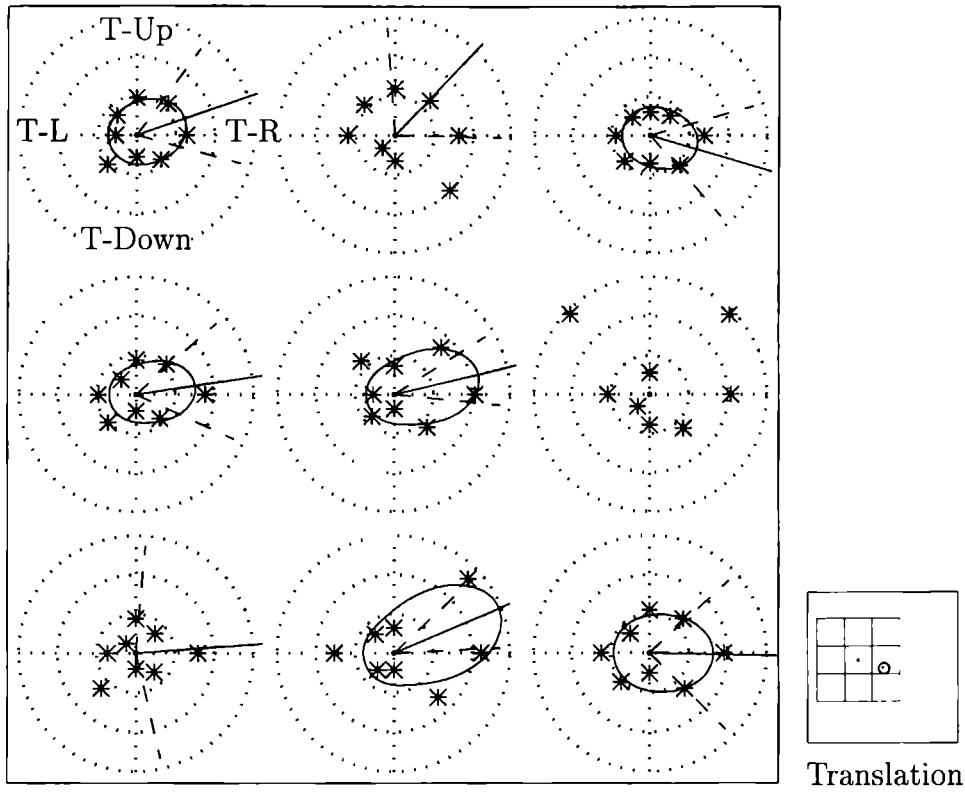


Figure 2.9: *Responses of expansion neuron J7 5 to translating stimuli presented in 8 different directions over each of 9 sub-fields of the RF. The stars represent the responses in the eight translation directions. For six sub-fields there was a significant direction tuning (Batschelet fit) as is indicated by the solid tuning curves. The preferred direction could be calculated for eight sub-fields, and is indicated by the solid line emerging from the center. The dashed line represents the accuracy of the direction tuning (2 SD). The outer circle corresponds to an AFR of 24 Hz. Note that the responses in the sub-fields were significantly lower than for the total field stimulus (Fig. 2.6) where the outer circle represents a response of 80 Hz. This low response level (also relative to background) explains the poor performance of the fitting algorithm for some sections of the RF. For the area around the fixation point (right, middle) the neuron showed a significant bi-directional translation response*

To investigate the neuron illustrated in Figs 2.10 and 2.11, the full expansion pattern was subdivided either into 4 (Fig. 2.12, middle) or 9 sections (Fig. 2.12, right), which were presented separately. As seen in Fig 2.12C, the neurons kept responding even when

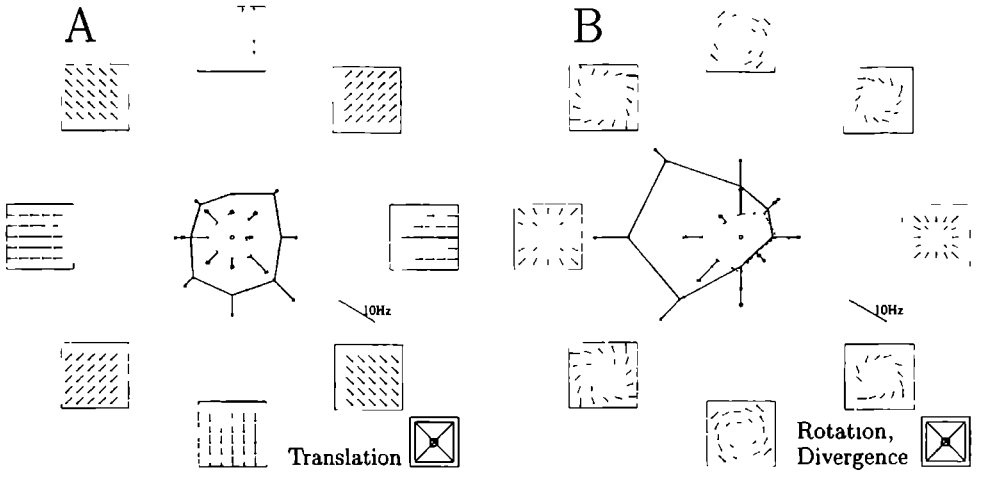


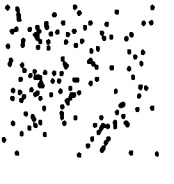
Figure 2.10: *Responses of a VIP neuron (Neuron D3.1) to translation (A) and divergence/rotation components (B). Conventions as in Fig. 2.6. Note that adding rotation to the expanding flow field caused only a minor decrement in response (upper and lower left stimulus in the right figure). The response curve was fitted with the Batschelet distribution. These were used in the example shown in Fig. 2.3.*

only small subsections of the RF were stimulated. Furthermore, there was no indication that the periphery was more powerful than the center for VIP neurons which are sensitive to divergence.

Spiral neurons

To investigate whether there are VIP neurons with special sensitivity to combinations of rotation and divergence ("spiral" stimuli), a subset of neurons was presented with this type of stimuli. In the present study the spiral stimuli were optimal for 9 of the 34 neurons tested with 8 conditions (see above). An example of such a spiral neuron in VIP is shown in Fig. 2.13.

Note that for this example, as for the other neurons in the "spiral group" (neurons for which the spiral stimuli yielded maximum responses), the selectivity for spiral stimuli was not very strict. All the neurons in this group showed sizable responses to other optic flow components as well.



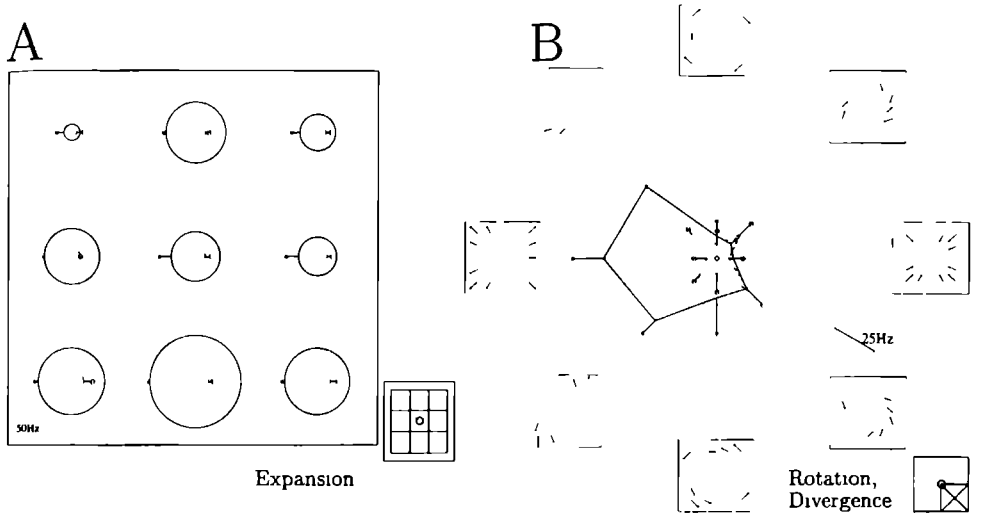


Figure 2 11 *Graph A shows a position scale test of expansion responses of VIP neuron D3 1 The stimuli were shown in a 3x3 grid of size 38° x 34° each (inset at bottom right) A complete expanding flow field was shown for each of the 9 locations tested, as indicated by each dotted "x" in the right lower corner The size of the stimulated area is indicated by the dotted square for the left upper corner The radius of the solid lined circle corresponds to the response level The dashed line represents the mean background activity during half a second before stimulus onset The error bars indicate the standard deviation B Responses of VIP neuron D3 1 to diverging and rotating stimuli presented over lower-right corner of the screen as indicated by the crossed area The field size was 72° x 64° The fitted values for the divergence/rotation Batschelet distribution are* $\phi_0 = -179\,7° \pm 8\,3$, $FMR = 65\,4 \pm 7\,3$ *Hz and* $TW = 61\,2° \pm 5\,5°$ *Were* $F = 9\,4$ *and* $p = 0\,049$

2.4 Discussion

In primate parietal cortex, the ventral intra-parietal area (VIP), located in the fundus of the intra-parietal sulcus, has been shown to contain neurons which are well-suited to integrate information about self-motion from several sources, including somatosensory and visual input Neurons in this region respond to tactile or visual stimuli, potentially corresponding to objects moving towards the animal (Colby et al , 1993b) In the present study, the somatosensory input to this area was confirmed In addition it was found that, in agreement with previous studies (Colby et al , 1993b, Duhamel et al , 1991), there is no saccade-related activity in VIP neurons However some neurons respond during smooth pursuit in darkness

A primary new result of the present study is the finding that neurons in VIP respond

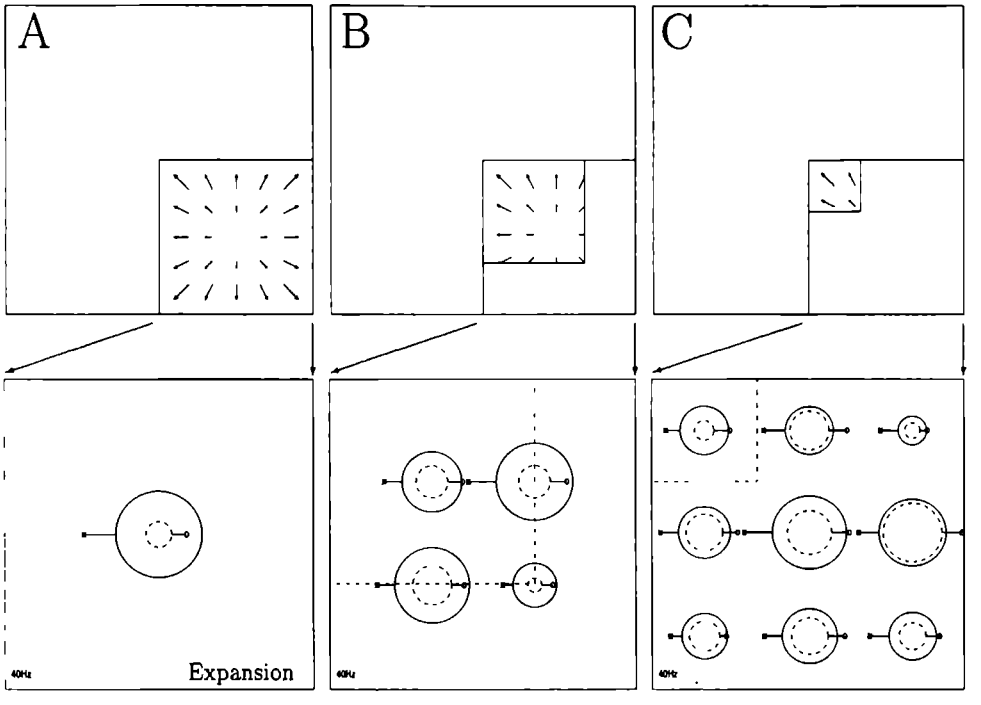


Figure 2.12: *Effect of masking on responses of VIP neuron D3.1 to expansion presented in the lower right field. For the data shown in the middle and right part of the figure, only sections of the stimulus were shown. The size of each section is indicated by the upper left dotted square in the middle and right drawing (masking experiment). The responses are plotted in the center of the area where the stimulus is shown. Note that 1 section in graph B overlaps 4 sections of the ones in graph C. The stimulus size for the largest complete non-masked stimulus (A) was 72° x 64°, the smallest area tested was 24° x 21° (C). For this masking experiment the responses were first tested over the same sensitive region of the RF as used for Fig. 2.11B. This sub-field proved to elicit much higher responses than stimulating the whole field (compare the responses to expansion in Fig. 2.10B).*

well to first order optic flow components, especially expansion. This finding fits well with preliminary communications of other groups on VIP of monkey (Graf et al., 1995) and man (Kennedy et al., 1995). To be effective, the self-motion component in the optic flow has to be linked to information from efference copies and proprioceptive input (vestibular, muscle spindles, etc.) and this could well be the role of VIP. Neurons in MT project both to MSTd and VIP and are sensitive mainly to translating stimuli, to which they respond in a direction selective manner (Maunsell and van Essen, 1983b; Albright, 1984). Nevertheless, MT neurons can respond to optic flow fields more complex than

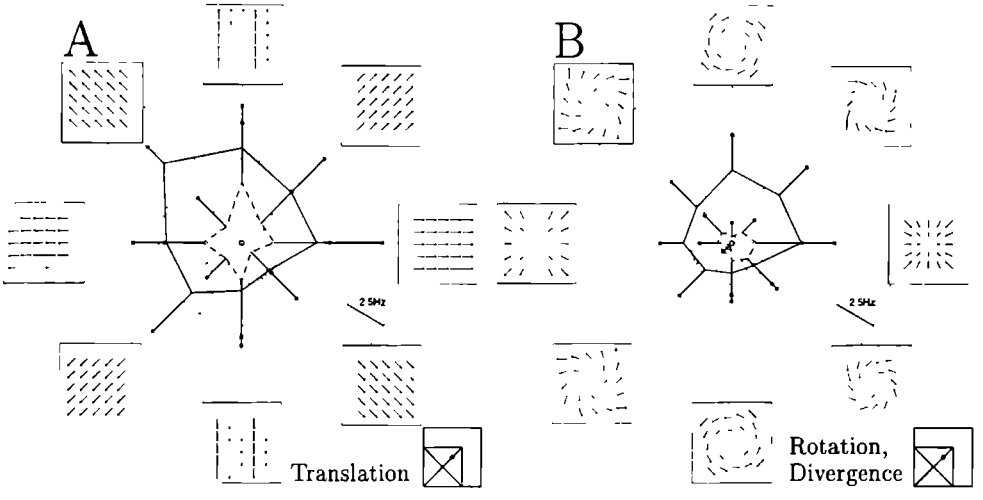


Figure 2.13: *Comparison of responses of VIP neuron L5.1 to translation (A) and first order optic flow stimuli (B). Conventions as in Fig. 2.6.*

translation, but only when these flow fields contain translation components presented over the RF (Lagae et al., 1994). In contrast to VIP or MSTd neurons, those in MT do not respond to presentations of optic flow components over subsections of the RF (Lagae et al., 1994). The responses of many VIP neurons to optic flow stimuli are therefore most similar to those observed by others in MSTd. This could be due either to a similar type of internal processing of incoming MT input in both areas or alternatively to transmission of MSTd input to VIP. In view of this question it is essential to first compare the optic flow responses in the latter two areas in more detail.

Similarities and differences between MSTd and VIP

Both VIP and MSTd neurons have mostly large RFs, and both respond well when presented with expanding or rotating dot patterns over their RF (Tanaka et al., 1986; Komatsu and Wurtz, 1988b; Duffy and Wurtz, 1995).

Secondly, VIP shows a predominance of responses to expansion. This is similar to related studies indicating a general preference of MSTd neurons for divergence (Duffy and Wurtz, 1995; Tanaka and Saito, 1989; Andersen et al., 1993; Lagae et al., 1994). Third, both MSTd and VIP neurons show "scale invariance" for the direction selectivity to first order optic flow components. Neurons in MSTd keep responding when an optimal stimulus, such as rotation or divergence, is scaled down and presented over a smaller section of the RF (Duffy and Wurtz, 1991b, Andersen et al., 1993; Graziano et al., 1994). This feature is considered to be specific for MSTd neurons (Lagae et al., 1994).

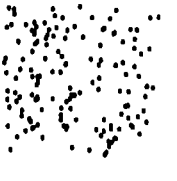
Fourth, both in MSTd (Tanaka and Saito, 1989) and VIP (this study) it is sufficient

to show only a small subsection of an expanding optic flow pattern to activate radial sensitive neurons Fifth, combinations of divergence and rotation ("spiral stimuli") are effective both in VIP (present work) and in MSTd (Graziano et al , 1990, Graziano et al , 1994) Sixth, both in MSTd and in VIP the responses of the neurons to first order optic flow patterns are quite resistant to variations in speed and size of the dots in random dot patterns (Tanaka and Saito, 1989, Duffy and Wurtz, 1991) Seventh, both in VIP (Colby et al , 1993b, Duhamel et al , 1991, this study) and in MSTd (Newsome et al ,1988, Dursteler and Wurtz, 1988) there are neurons which respond to smooth pursuit eye movements even in darkness

Apart from the somatosensory input, a main difference between MSTd and VIP lies in the absence of single component neurons in VIP In MSTd a small proportion of the neurons is only activated by a single first order optic flow component Duffy and Wurtz (1995) termed these neurons planar (P), radial (R) and circular (C) neurons and found that they represented 8, 8, and 2 percent of the population respectively In contrast the neurons in VIP were sensitive to several first order optic flow components Additionally, they could always be driven by translating stimuli One should keep in mind, however, that the present sample of neurons was smaller than the one of Duffy and Wurtz (1995), and that different selection criteria were used to classify the neurons in the 2 laboratories Chapter 5 will show that some VIP neurons exhibit little response to simple translation, but are responsive if the same translating stimuli are oscillated across the RF Hence, the observation that all the VIP neurons were driven to some extent by translation may have been more related to my extensive search for such responses than to a basic difference between VIP and MSTd

A second possible difference between VIP and MSTd is that movement in the non-preferred direction frequently elicits suppression in MSTd neurons (Duffy and Wurtz, 1991a, Graziano et al , 1994) while this was seldom observed in the present study on VIP, that is, if one looks at AFR (average firing rate) In some neurons, there was a short-lasting suppression of the background followed by a tonic facilitatory response while stimulating in the non-preferred direction (NPD) These effects canceled each other out, resulting in an AFR response which was not significantly different from the background activity Another factor contributing to this apparent difference is the relative absence of single component neurons For the latter neurons it is easier to find a stimulus which is purely opposite to the optimal one and thus completely suppressive In contrast, for multiple component neurons, a stimulus in the NPD is likely to contain components which facilitate rather than suppress the neural response

A third difference between VIP and MSTd concerns the observation that the periphery of the RF has a special significance for MSTd while this is less so for VIP For example, one of the most interesting results of Tanaka and Saito (1989) was that the response to expanding patterns persisted even if only a peripheral annulus of the pattern was shown (their Fig 3) Masking the central part had surprisingly little effect, while masking the periphery made the responses disappear In the experiments presented here, there is no equivalent to the center being masked in isolation However, by showing only the center of the stimulus and not periphery, an experiment was done which closely mimics the center-without-annulus experiment of Tanaka and Saito (1989) In VIP such experiment



does not lead to the response being abolished However, it remains to be seen whether this reflects a genuine difference between these areas or whether this is due to a difference in potency of the stimuli used in the 2 laboratories

Overall, the similarities between VIP and MSTd are much more striking than the differences This is especially true with respect to "scale invariance "

Scale invariance

Position invariance is a neuron's consistent selectivity to a stimulus regardless of where the stimulus falls in the neuron's receptive field (Graziano et al , 1994) The general method to test neurons for position invariance, is to show the optimal and non-optimal stimulus over sub-fields of the receptive field In MSTd the number of sub-fields tested varied considerably between the different studies (N=4 (Saito et al , 1986), N=2-3 (Duffy and Wurtz, 1991b), N=25 (Lagae et al , 1994), N=5 (Graziano et al , 1994)) Although scale invariance is but one aspect of position invariance, it is of interest to compare the relevant data in VIP and MSTd

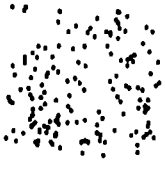
In the present study it was shown that scaled-down versions of the optimal stimulus presented over 9 subsections of the field was surprisingly effective in activating VIP neurons The data show, that by stimulating only 11 1 percent of the original stimulus area, the response was on average about 64 percent of that of whole field stimulation (93 percent for the best sub-field)

Position invariance is considered to be specific for MSTd neurons, and is not seen in MT neurons (Lagae et al , 1994) For MSTd, it was recently pointed out by Duffy and Wurtz (1995) that this invariance was relative rather than absolute For example, when the same divergence pattern is presented over different parts of the RF, there are usually positions where the responses are distinctly larger Hence, a sensitivity profile can be constructed (see Lagae et al , 1994), which explains the finding of Duffy and Wurtz (1995) that neurons with radial sensitivity have a graded preference for centers of motion

The present study reveals that other factors may contribute as well The presentation of a small peripheral section of an expanding pattern is sufficient to elicit a maximum response From this it can be understood why expansion sensitive neurons appear so robust with respect to displacement of the center of expansion (Graziano et al , 1994) From the present data, it is evident that neurons of this type can react even if the focus of expansion is outside the most sensitive area of the RF However, this does not mean that these neurons are not able to code for the focus of expansion (see also Lagae et al , 1994)

Mechanisms underlying sensitivity to first order optic flow in VIP

According to the classification of Duffy and Wurtz (1991b), there are basically two types of hypotheses to explain sensitivity for radial and circular motion The direction mosaic hypothesis and the vector field hypothesis The direction mosaic hypothesis assumes that the RF consists of a patchwork of sub fields which are sensitive to planar motion and



which vary in preferred direction depending on the type of neuron For radial "expansion" neurons, all sub-fields have a preferred direction pointing outwards from the center of the field For spiral neurons, the preferred directions should be arranged in a spiral etc In the present study, this hypothesis was tested directly by presenting local translations in various directions over the sub-fields of the RF of VIP neurons It was found that none of the neurons had sub-fields arranged as predicted by the direction mosaic hypothesis Instead all neurons kept the same direction selectivity for translation irrespective of the position of the sub-field in the larger RF The present data are better accommodated by what Duffy and Wurtz (1991b) termed the vector field hypothesis, which is basically similar to the compartment model proposed by Saito et al (1986) In these and related models (Zang et al , 1993) the local detection of rotation or divergence is achieved by projections of the appropriate afferents onto single branches of neurons

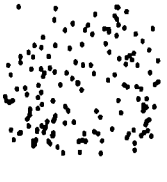
A special case is the sensitivity to spiral stimuli In MSTd there is an ongoing debate about the presence of neurons with special sensitivity to spiral stimuli In contrast to pure radial neurons, which show a decrease in response when expanding patterns are mixed with rotation (Orban et al , 1992), spiral neurons are preferentially activated by spiral motions, which combine both expansion/contraction and rotation components Graziano et al (1990,1994) found many examples of this type in MSTd, while others found them very rarely (Lagae et al ,1994) For some VIP neurons a spiral pattern constitutes the optimal stimulus Nevertheless it would not be appropriate to label these neurons as "single component" spiral neurons since they clearly are responsive to other optic flow components as well

Functional considerations

Two hypotheses have been proposed with respect to the functional role of parietal neurons in the analysis of optic flow According to the 'navigational' hypothesis, the responsiveness to optic flow patterns makes these neurons well-suited for visual guidance during egomotion (Roy and Wurtz, 1990, Saito et al , 1986) The large size of RFs and the predominance of expansion neurons (forward locomotion is more common than backward) are in favor of the suggestion that neurons in MSTd and in VIP can help in navigation during self-motion However, as was pointed out by Graziano et al (1990,1994), there are several discrepancies within this hypothesis For example, although some MSTd neurons respond to full field stimuli, their RFs are not always large and sometimes are in the order of 10 degrees across In agreement with Graziano et al (1990,1994), the present data on area VIP indicate that neurons with such apparently 'small' RFs are able to respond to full field stimuli as well, but their response improved when the most sensitive part of the RF was stimulated selectively Similarly Duffy and Wurtz (1991b) found their MSTd neurons to be responsive to 100° x 100° stimuli, irrespective of their RF size

Hence, those and the present data of area VIP can also be viewed as supporting the 'motion pattern' hypothesis, which states that MSTd neurons are involved in the analysis of motion of individual objects (Sakata et al , 1985, Sakata et al , 1986) Actually, in many cases there is a combination of local and global motion In the real world, every

approaching object contains local texture features which also exhibit expansion Therefore, the detection of local expansion by VIP neurons can contribute to the detection of more global expansion, covering the whole RF This leads to the conclusion that the response to full field stimulation in VIP neurons clearly indicates that such neurons could contribute to a global (egomotion) analysis of the surround However, stimuli shown over small portions of the RF (figures 2 10 and 2 11) elicit sometimes even higher responses than the stimuli shown over the whole RF This suggests that some VIP neurons may play a dual role detection of egomotion as well as object motion in the 3-D space



Chapter 3

Responses in VIP to translation and fanning optic flow

3.1 Introduction

Saito et al (1986) showed that some neurons in MST are primarily responsive to rotation of planes in depth ('Rd' neurons, Fig 3 1) Sakata et al (1983, 1986) found this same type of neurons in an area, which was later (Komatsu and Wurtz, 1988b) identified as MST VIP receives input both from areas MST and MT (Boussaoud et al ,1990, Baizer et al ,1991) Previous physiological studies (summarized by Duhamel et al , 1991 and Colby et al , 1993b) have shown that neurons in VIP give direction selective responses to whole-field translation of random-dot patterns However, so far there have been no reports on VIP sensitivity to rotation in depth In this chapter such sensitivity will be explored, occasionally with real textured stimuli but more often with quantitatively controlled optic flow patterns on a tangent screen

When a plane is slanted relative to the observer starting from a fronto-parallel position, the optic flow corresponds to a vector field called fanning (Kanatani, 1987) Together with translation, divergence, rotation and shear, fanning enables us to describe every possible flow field generated by a flat surface moving in space Translation, divergence and rotation have been known to be potent stimuli for both MST (Tanaka et al , 1986, Saito et al , 1986, Tanaka and Saito, 1989, Tanaka et al , 1989, Duffy and Wurtz,

Adapted from S J Schaafsma, J Duysens and C C A M Gielen, Responses in ventral intra-parietal area of awake macaque monkey to optic flow patterns corresponding to rotation of planes in depth can be explained by translation and expansion effects Visual Neuroscience, Vol 14, 1997, pages 633 646

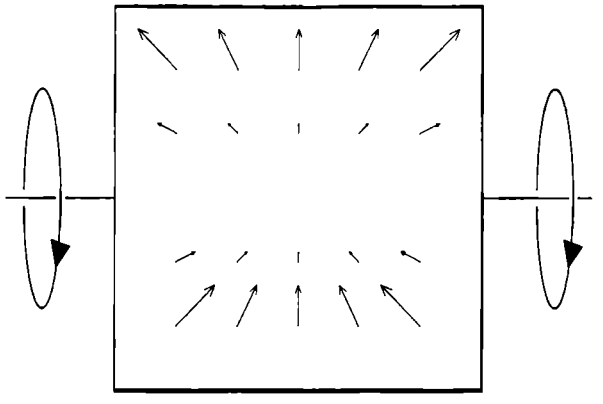
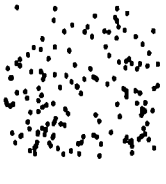


Figure 3.1: *'Rotation in depth' stimulus. Note that the upper half of the pattern moves towards the observer. This creates locally an expansion of texture. When the plane is exactly fronto-parallel, the instantaneous flow field is a pure fanning.*

1991a; Duffy and Wurtz, 1991b; Orban et al., 1992; Graziano et al., 1994; Lagae et al., 1994) and VIP (Chapter 2). Here, the VIP responses to these stimuli with those to fanning will be compared, in order to search for cells with possible specializations towards fanning.

Translation is generated by a fronto-parallel plane moving perpendicular to the line of sight. Rotation is generated by a plane rotating around the line of sight. Divergence gives the impression of a fronto-parallel plane moving towards (expansion) or away (contraction) of the observer. Fanning gives the subjective impression of a fronto-parallel plane, which is continuously tilting without changing position. This impression is created by a group of dots (each with a finite life-time) which appear to form a large moving plane starting to rotate in 3D (around a fronto-parallel axis of rotation positioned in the middle of the imaginary plane; Fig. 3.1). Since the structure of the flow field is not changing over time for fanning (e.g. there are no clear edges at the border of the plane with random dots), these stimuli avoid some of the complexities of the optic flow of a real plane actually rotating. In the case of a real plane, the orientation of the plane changes during rotation and the total area covered by the stimulus varies from a maximum size to a thin line (when the plane lies in the line of sight). It is important to note that a fanning stimulus as used here, does not change in size, and the corresponding plane does not change its orientation in space. Therefore, the fanning stimulus does not resemble the actual complete movement of a plane over time, but rather represents the flow field corresponding to the start of that movement.

For fanning the translation component is zero along the fronto-parallel axis of rotation of the textured plane. For further analysis two degrees of freedom are left to describe the fanning stimulus: the orientation of the fronto-parallel axis and the average speed



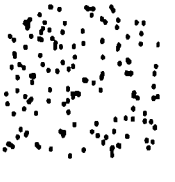
of the pixels within the stimulus As will be shown below, this can be nicely linked to both translation (mean direction of the flow) and divergence With this set translation, divergence, rotation, deformation, and fanning, every optic flow field generated by the most simple shape in 3D, a plane, can be fully described For a fronto-parallel plane rotating in depth (Fig 3 1), there is an expansion component in the upper half of the plane which is approaching the observer, while in the lower half there is a contraction component Also, on the left half side there is a counterclockwise rotation, whereas at the right half side there is a clockwise rotation This optic flow pattern matches exactly with fanning when the fronto-parallel plane starts to move As soon as the plane is slanted, additional first order components are required to describe the optic flow completely A neuron which is optimally sensitive to rotation in depth would have a combined local responsiveness to both expansion and contraction and would also respond to a more global fanning pattern Such neurons have not been described so far in MST or VIP However, it has been demonstrated that MST neurons often have different local sensitivity profiles for expansion and contraction (Lagae, 1991)

It is easy to imagine that fanning stimuli can be particularly effective for MST neurons, provided that the fanning stimuli are properly positioned over the receptive field (Sakata et al , 1983, Sakata et al , 1986) Similarly, in chapter 2 it was shown that VIP neurons resemble MST neurons in their responses to translation and that they are sensitive to expansion/contraction, even with position invariance Hence VIP neurons may be expected to respond to fanning as well Since fanning has also a strong translational component (for example a mean upward translation in both upper and lower part of Fig 3 1), it is also possible that the responses to fanning are determined by the translational direction selectivity Finally, it is conceivable that neurons responsive to fanning form a separate group In that case, one would expect the responses to fanning to be much larger than that to other optic flow components or at least their tuning should be sharper than the tuning for translation

The responses to computer-generated fanning flow fields were compared to those obtained following the presentation of other basic optic flow stimuli to investigate whether VIP neurons, responding to fanning, belong to the same categories as described by others using diverging or rotating optic flow stimuli, or whether they form a separate class within VIP, similar to the group described by Saito et al (1986) for MST Since neurons in VIP are especially sensitive to nearing objects (Colby et al , 1993b), one would expect these neurons to react to optic flow patterns containing not only divergence but also rotation in depth The MST input would be well-suited to provide such input

3.2 Methods

The responses of VIP neurons were recorded from two awake male monkeys (Macaca Mulatta, weighting both around 6 kg) Preparation, stimuli, experimental paradigm, recording technique and off-line analysis were the same as described in chapter 2 Additionally, there were fanning stimuli presented in eight directions These directions corresponded to fronto-parallel axes at angles of 0, 45, 90, 135, 180, 225, 270, 315 de-



grees with respect to the vertical The subjective impression of the fanning stimuli is one of seeing a slightly tilted moving plane positioned in 3D, which is starting to rotate along the fronto-parallel axis of rotation (Fig 3 1)

When a plane is slanted relative to the observer, one can describe the resulting optic flow pattern locally in a unique way by a set of optic flow components derived from its Taylor expansion The zeroth order component of the flow field corresponds to the translation The first order component corresponds to divergence, rotation or deformation (spatial derivatives under rotation invariance, Koenderink and van Doorn, 1975) A description of all the optic flow patterns that are generated by a plane moving in a 3D environment can not be given in terms of these zeroth and first order optic flow fields alone Kanatani (1987) has proven that for a complete solution of the structure-from-motion problem for a moving plane, one needs in addition to the zeroth and first order flow fields a second order flow field which was termed fanning Fanning is the optic flow corresponding to a frontoparallel plane that rotates around a frontoparallel axes Again, as in the previous chapter, the data was fitted by a Batschelet distribution (Batschelet, 1981) Figure 3 2 shows on the left side the original data (A), on the right side the resulting fit by using the Batschelet distribution (B) The fitted profile was response $= b\,exp(k\,cos(\phi - \phi_0 + \nu\,sin(\phi - \phi_0)))$ Here b, k, ν and ϕ_0 are the fit parameters and ϕ the direction of the flow in polar coordinates

3.3 Results

A total of 172 neurons were recorded from VIP (Table 2 1) Fifty-two neurons could be measured long enough to obtain quantitative tests with translation and several types of first order optic flow stimuli as reported in chapter 2 This chapter reports on the 31 neurons tested for fanning and other optic flow stimuli (translation and/or first order optic flow) Ten cells responded poorly but twenty-one neurons gave significant responses to both fanning and at least one of the first order optic flow patterns such as rotation, divergence and/or a combination of these components (Table 3 1) For 3 of these neurons there was no significant tuning in the response towards divergence or rotation or any combination of these stimuli For 10 neurons the optimal stimulus was expansion, for 1 it was contraction, for 2 rotation The other 5 responded best to spiral stimuli (combinations of divergence and rotation)

	Number of neurons	Optimal direction
	3	No significant tuning towards divergence/rotation
	10	Expansion
	1	Contraction
	2	Rotation
	5	Spiral stimuli (divergence and rotation)
total	21	

Tabel 3 1

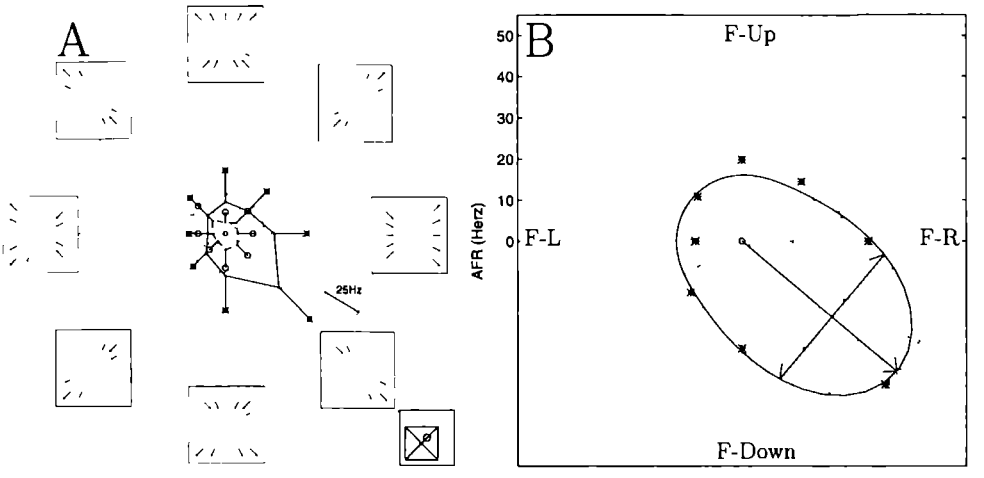


Figure 3.2: *A: Responses of a VIP neuron (Neuron N_1) to fanning. In the lower right corner the size of the stimulus area is shown. Here, the outer border represents the field of view of the monkey (117° x 113°), the inner square (with the diagonal lines) corresponds to the area stimulated (70.2° x 67.8°), the dot represents the fixation position. The data in this figure is plotted in a polar manner. The center corresponds to zero activity. The radial axis corresponds to the average firing rate (AFR). The angular dimension represents the direction of the translational component in the fanning. A 90 degrees angle in this plot means that both stimuli are orthogonal to each other (a 90° cw or ccw rotation of the stimulus results in the same flow field as the other). The solid line connects the AFR as measured during the whole stimulation period. The dashed line represents the mean background activity during half a second before stimulus onset. The error bars indicate the standard deviation. B: From the data shown in the left plot the direction tuning and the broadness of the tuning was calculated. The response curve is* $b\,exp(k\,cos(\phi - \phi_0 + \nu\,sin(\phi - \phi_0)))$ *with the fitted values* $b = 28.0 \pm 2.0$ *Hz and* $k = 0.55 \pm 0.06$ *and* $\phi_0 = -40.1° \pm 4.8°$ *and* $\nu = 54.4° \pm 15.9°$. *The fit resulted in an F of 20.9 (p=0.016). The tuning width is then* $69.3° \pm 1.5°$ *and the FMR is* 48.6 ± 2.0 *Hz.*

Amongst the 21 cells tested both with fanning and first order optic flow, 17 could also be tested with translation, enabling a comparison of the responses for both types of stimuli. These neurons fell into 2 groups. In the first group the RF was small and direction selective for translating stimuli, especially a small light bar. These neurons will be termed "MT-like VIP neurons". A second group had larger RF's and they were sensitive to first order optic flow components (expansion/contraction; rotation). These neurons will be termed "MST-like VIP neurons".

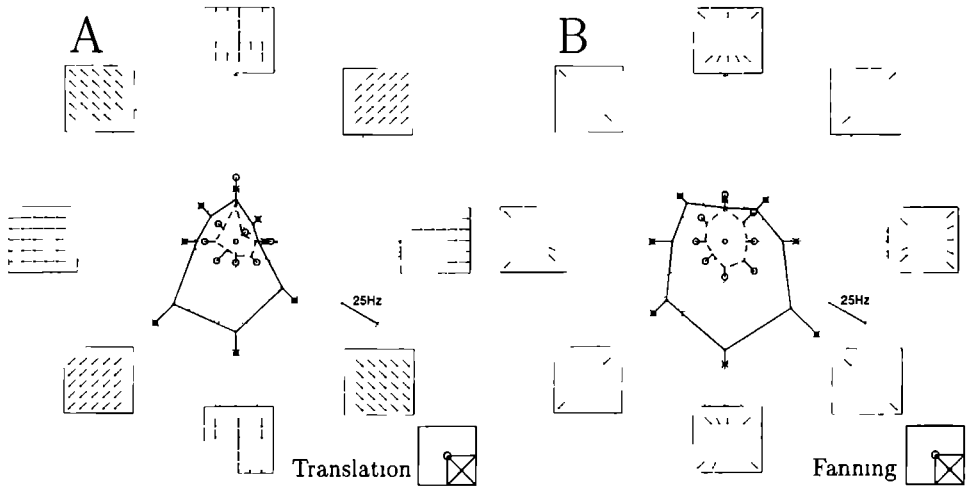


Figure 3 3 *Comparison of responses of MST-like VIP neuron (Neuron N_2) to translation (A) and fanning (B) In the right lower corner in each figure the size of the stimulus area is shown The outer border represents the field of view of the monkey (117° x 113°) The inner square (with the diagonal lines) corresponds to the area stimulated (58 5° x 56 5°) The small circle indicates the position of the fixation dot (middle of the screen) The data in this figure are plotted in a polar manner The center corresponds to zero activity The radial axis corresponds to the AFR The angular dimension represents the stimulus parameter (direction of translation) As translation (A), a 90 degrees angle in plot B means that both stimuli are orthogonal to each other The solid line connects the AFR as measured during the whole stimulation period The dashed line represents the mean background activity in a period of half a second before stimulus onset The error bars indicate the standard deviation The data points were simply connected to each other to obtain the summary plot*

MST-like VIP neurons with direction selective responses to translation

Most VIP neurons showed clear directional selectivity for both translation and fanning An example of such a neuron is given in Fig 3 3 The neuron gave strong responses to a dot pattern moving downward (Fig 3 3A, fitted maximum response, FMR = 61 0 ± 5 1 Hz, mean and SD) over the right lower quadrant of the visual field (inset in Fig 3 3A) When tested with fanning dots (Fig 3 3B, FMR = 67 2 ± 2 7 Hz) the neuron again showed clear direction selectivity The Batschelet fit yielded an optimal direction of −94 6 ± 7 4 degrees for fanning and −106 9 ± 3 2 degrees for translation Hence, it was presumably the translation sensitivity which dominated the sensitivity to fanning in this case

The main difference between the 2 tuning plots in Fig 3 3 is the presence of larger responses for directions orthogonal to the preferred direction for fanning compared to that for translation It should be noted that in the fanning stimulus directed to the left and the right, there is a downward translation component This translation fraction could explain the difference in the shape of the plots Note that the difference is not in the broadness of both curves but rather in the shape (broadness in Batschelet fit was 70 2° ± 1 8° for fanning and 71 1° ± 0 8° for translation) The cell shown in Fig 3 3 (cell N_2) was the most extreme example of a cell showing this phenomenon, but 20 percent of the cells showed a similar tendency

The same neuron was also tested for rotation and expansion/contraction stimuli and combinations of these two types of stimuli ("spiral") The optimal spiral stimulus was a combination of clockwise rotation and convergence The results are shown in Fig 3 4 In analogy with the scheme of Graziano et al (1994) for MST neurons, this VIP neuron could be classified as a spiral neuron (Fig 3 4) Five cells of the 21 neurons responding to first order optic flow could be classified as being a spiral neuron (Table 3 1)

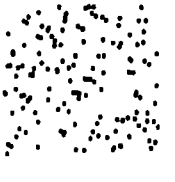
Mechanisms underlying the direction selectivity

Given the preferences for some types of fanning and spiral stimuli, the question came up as to how the structure of the RF could accommodate these complex stimuli Based on the considerations given above one could expect that all parts in the RF were sensitive to downward translation, but one might also expect that some parts of the RF had different sensitivities and different preferred directions for translation, in order to explain the sensitivity for spiral stimuli To explore the structural basis of the direction selectivity, the translating stimuli were subdivided in 9 subsections This allowed the testing of 9 parts of the RF with translation in 8 different directions The results of such a test, applied to neuron N_2 from Figs 3 3 and 3 4, are shown in Fig 3 5

In general the reduction in stimulus size results in a decrease of the response strength As a consequence a larger number of sweeps is necessary in order to obtain a good Signal-to-Noise ratio Fig 3 5 shows that sufficient data were obtained to construct tuning curves for 7 out of the 9 subsections with a clear directional tuning In all 9 subsections there was a preference for downward movement, consistent with the sensitivity of the whole field In one subsection (bottom right), the preferred direction clearly deviated to the left This direction corresponds roughly with the mean flow direction in the same corner of the optimal spiral stimulus (Fig 3 5) For this cell, this was the only instance in which the RF substructure seemed to support the sensitivity for an optimal stimulus in the whole RF This test was done on four other translation tuned neurons, all showing the same preferred direction for the subfields as for the complete receptive field

MT-like VIP neurons

In MT-like VIP neurons, it was hard to test neurons with dot fields These neurons had relatively small receptive fields and responded well to a moving light slit Most often there was barely a response to random dot stimuli and the responses gave the impression that



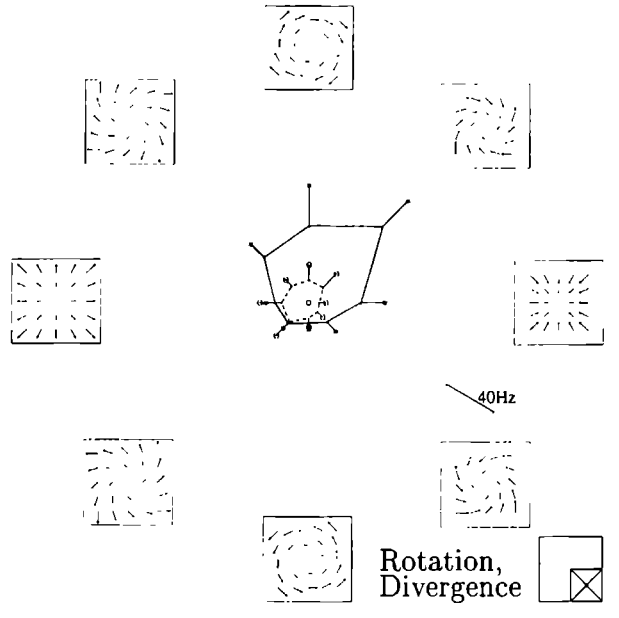


Figure 3.4: *Responses of a "spiral" MST like VIP neuron (Neuron N_2) to divergence/rotation. The data in this figure are plotted in a polar manner. The center corresponds to zero activity. The radial axis corresponds to the AFR. The angular dimension represents the stimulus parameter: divergence, rotation or a linear combination of these principal flow components. As in the plot for translation and fanning, (Fig. 3.2 and 3.3) a 90 degrees angle in this plot means that both stimuli are orthogonal to each other. The solid line connects the AFR as measured during the whole stimulation period. The dashed line represents the mean background activity in half a second period before stimulus onset. The error bars indicate the standard deviation. Note that combining a contracting and a clockwise rotating flow field ("spiral" stimulation) resulted in the optimal response (upper right stimulus). In the lower right corner in the figure the size of the stimulus area is shown. The outer border represents the field of view of the monkey (117° x 113°). The inner square (with the diagonal lines) corresponds to the area stimulated (58.5° x 56.5°).*

individual dots, rather than the whole stimulus, were the driving stimulus. Figure 3.6 shows an example of the responses of such an MT-like VIP neuron.

In MT-like VIP neurons the optimal direction for fanning (Fig. 3.6C; $\phi_0 = -16.0° \pm 4.5°$) was also quite well predicted by the preferred direction for translation (Fig. 3.6A; $\phi_0 = -29.4° \pm 12.2°$). The best response to fanning was slightly smaller than the best response to translation. The responses to the random dot fields were very noisy and showed a sharp tuning in one direction for translation. Note that there was also a small response to expansion (Fig. 3.6B), but the latter response

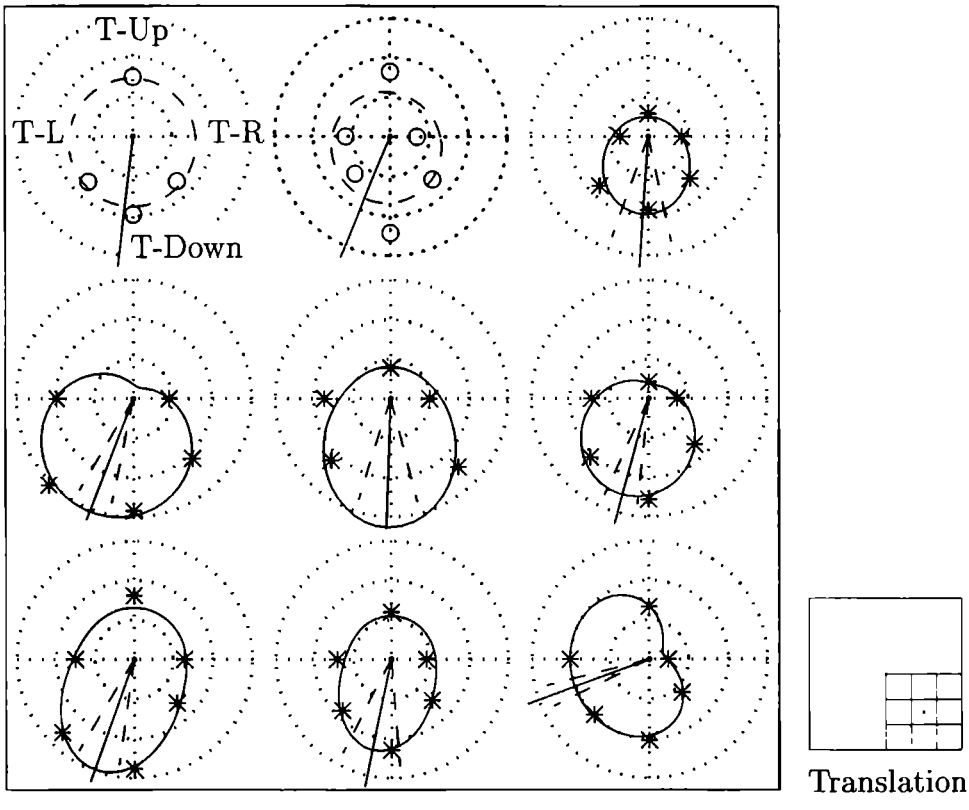


Figure 3.5: *Responses of a "spiral" MST like VIP neuron (Neuron N_2) to translating stimuli presented in 6 different directions (0, 90, 180, 225, 270, 315, deg.) over 9 subfields of the RF. For seven subfields there was a significant direction tuning (Batschelet fit) as is indicated by the solid tuning curves and stars. For the upper left and middle subfields there was no significant tuning. The preferred direction of the subfields is indicated by the solid line emerging from the center. The "striped" line represents the accuracy of the tuning (2 SD). The scale of the nine subfields is the same for all plots. The outer circle corresponds to an AFR of 100 spikes/s.*

was not position invariant.

For MT-like VIP neurons, the small receptive field made it hard to locate the center of the RF by hand-driven stimuli. Therefore, the center of the expanding flow fields was rarely located exactly over the center of the receptive field. Careful examination with additional tests revealed that for the MT-like VIP neuron shown in Fig. 3.6, the most sensitive part of the RF was slightly displaced with respect to the center of the stimulus as shown in the figure. For the expansion stimulus used in Fig. 3.6B, the most

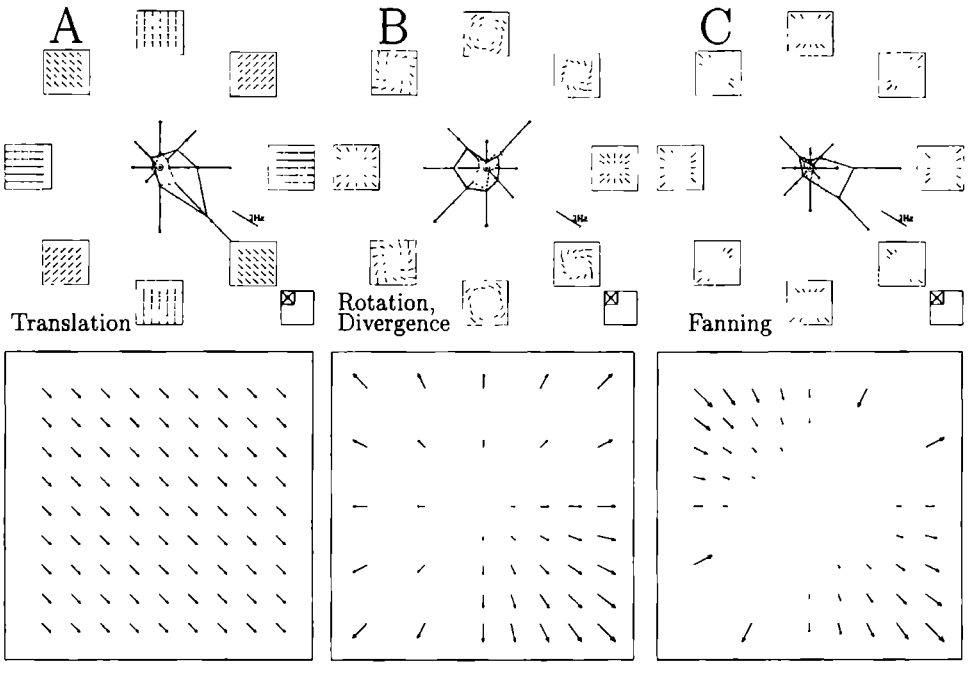


Figure 3.6: *Responses of MT-like VIP neuron (Neuron N_3) to translation (A), divergence/rotation (B) and fanning (C). Bottom: schematic representation highlighting those parts of the optimal stimulus in A,B and C, which provide translational components in the preferred direction. The denser vectored areas represent those where the flow of this optimal stimulus was in the direction ($\pm$ 45°) of the optimal translation direction (A).*

sensitive center of the receptive field was stimulated with dots moving towards this lower right corner (as illustrated at the bottom of Fig. 3.6B, in which the stimuli over the lower right corner are accentuated). As translation in this direction was optimal for this neuron (Fig. 3.6A), it can be concluded that the sensitivity of this neuron for expansion could be explained on the basis of the translation sensitivity. This is similar to observations of Lagae et al. (1994) in MT, who found that MT neurons can be made to respond to expanding optic flow fields, provided that the stimulus is positioned such that the translation-sensitive RF is activated by the appropriate section of the divergent pattern.

Similarly, the sensitivity for fanning may have resulted from the positioning of translation components in the stimulus over the most sensitive part of the RF. This idea is illustrated at the bottom of Fig. 3.6C. It can be seen that translation in the preferred direction is a prominent component in two sections of the RF. One of these sections (bottom, right) was shown over the most sensitive part of the RF, thereby providing a possible basis for the responsiveness to fanning of this neuron. Two neurons were

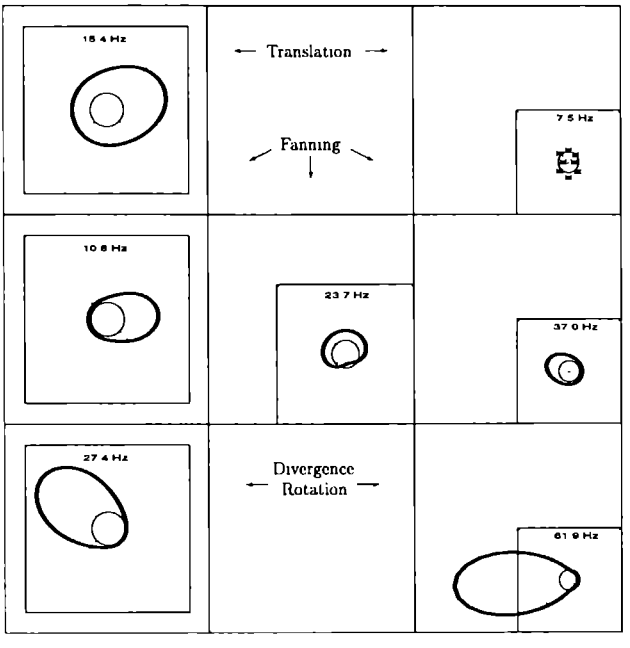
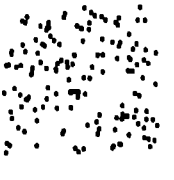


Figure 3.7: *Fitted tuning curves of VIP neuron N_4 to the various basic optic flow components presented over the whole field and to the lower right contralateral field. Translation (top) and Rotation/divergence (bottom) was measured on two positions, Fanning on three (middle). The outer border of each of the panels represents the field of view of the monkey (117° x 113°). The inner square (with the diagonal lines) corresponds to the area stimulated (left: 93.6° x 90.4°; middle:78.0° x 75.3°; right: 58.5° x 56.5°). The inner circle represents the background activity, the thick solid line the tuning curve based on the responses relative to the background. The maximum response for each condition is shown.*

identified as being "MT-like", one could be termed bi-directional.

For one cell (N_4), the response to fanning was studied while scaling down to the most sensitive region of the RF. Tested for the whole RF, neuron N_4 showed the same direction selectivity for both translation and fanning (Fig 3.7, left graphs). The optimal stimulus was a combination of divergence and clockwise rotation (Fig 3.7, lower-left graph). When the stimuli were scaled down to the most sensitive part of the RF, there was an increase in the response for the expansion stimulus (Fig. 3.8, lower-right graph). At the same time the direction tuning for the fanning stimulus started to shift, while the response increased. There was no significant tuning for translation in the most sensitive part of the RF.



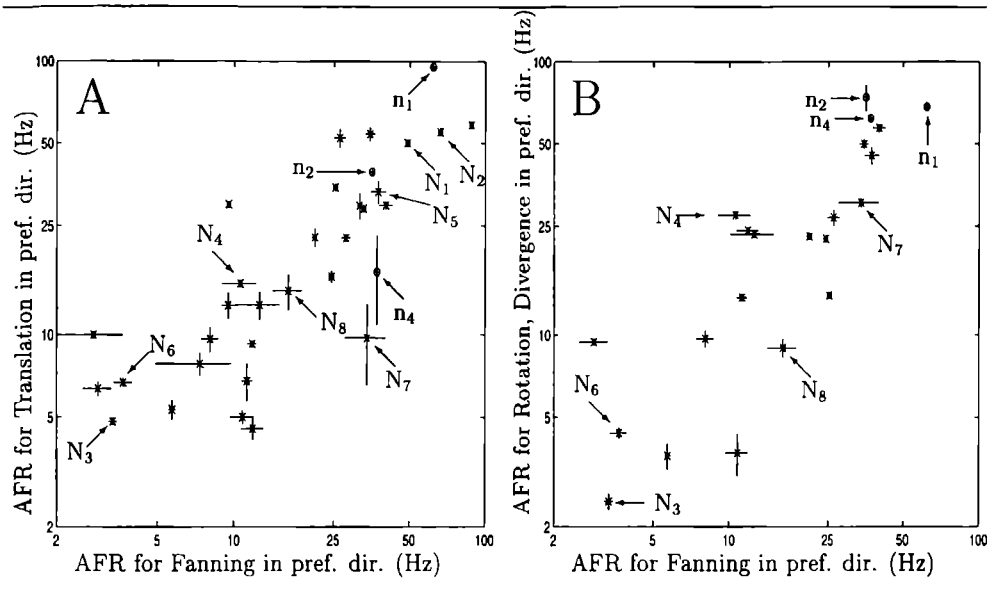


Figure 3.8: *Comparison of average responses in the preferred direction for fanning with those for translation (A) and divergence/rotation (B). Lines indicate standard error. The neurons illustrated in other figures and in the text (Neurons N_1, etc.) are indicated. Circles indicate that neurons are shown twice (see text).*

Are there specialized fanning neurons?

To investigate whether VIP neurons respond significantly better to fanning stimuli than to other types of stimuli, a comparative analysis for responses to fanning, translation and first order optic flow (such as shown in Figs. 3.3, 3.6 and 3.7) was performed for all neurons in the population. First, the best mean responses were plotted for all neurons tested with both fanning and translation (Fig. 3.8A). Most neurons were responsive to both types of stimuli. The plots were constructed based on the data from 30 neurons. The ratio of the standard deviation over the mean response was (σ_{AFR}/AFR) was 0.7. The responses to fanning and translation in the preferred direction for stimuli with the same mean velocity were compared. From the 30 neurons, none showed a significantly better response to translation than to fanning or vice versa. For 21 neurons the responses to divergence (div.) and rotation (rot.) were also tested (Fig. 3.8B). Overall the responses to fanning were slightly larger than those to div./rot. Two neurons had significantly ($p > 0.95$) larger responses for fanning than for divergence and rotation. Both neurons were identified as being "MT-like". By fitting the data following a Batschelet distribution (see chapter 2 methods and Batschelet, 1981) it was possible to determine both a preferred direction and a broadness of tuning as shown in Fig. 3.2. Similar plots were made for a series of neurons and used to calculate the preferred direction and tuning width (Fig. 3.9).

Figure 3.9 shows data only for those neurons for which enough data was available to

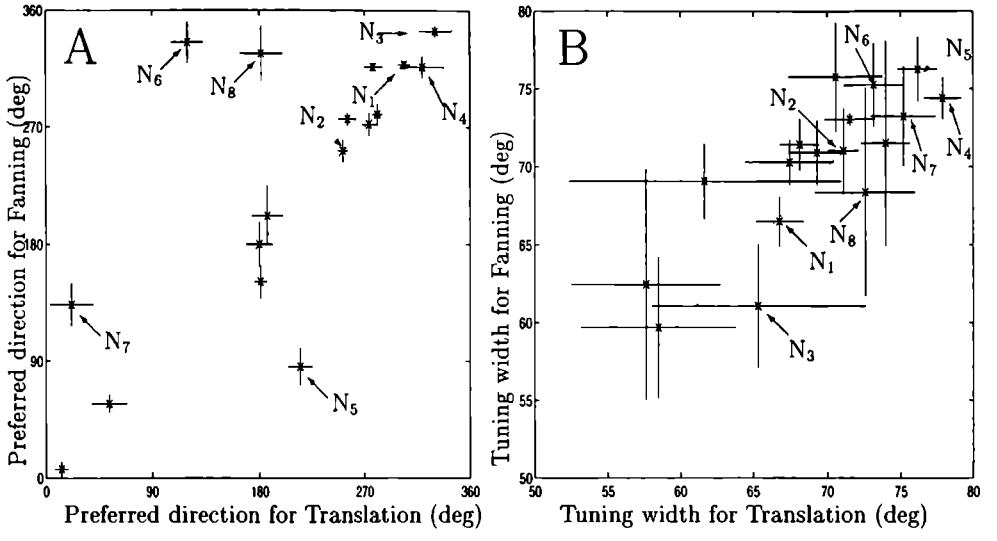


Figure 3.9: *Comparison between tuning direction (A) and tuning width (B) for translation and fanning after fitting the data to a Batschelet distribution (response* $= b\,exp(k\,cos(\phi - \phi_0 + \nu\,sin(\phi - \phi_0)))$*). The crosses indicate one standard deviation. The neurons illustrated in other figures and text (Neurons* N_1*, etc) are indicated.*

yield a fit for both translation and fanning (N=17). The tuning direction is basically the same for translation and fanning for all but four neurons (Fig. 3.9). After calculating the tuning curve based on the responses relative to the background, the tuning directions for translation and fanning are significantly different. Thus the difference for these four neurons can not be explained by variations in background activity. Three neurons (N_5,N_6, and N_7) share the property of a very broad tuning for the direction selectivity (Fig. 3.9B). This seems to correlate with a less precise match of tuning directions for translation and fanning. Broadly tuned neurons are hard to compare with respect to their direction tuning, using this or any other method.

Neuron N_8 has a bi-directional response profile (not shown). There was a preferred direction, but the direction perpendicular to it showed the second best response. The fit used here smoothed out this bi-directional behavior. It detected the preferred direction but indicated that the Batschelet curve did not do very well (F=1.7). The fit was still better than just taking the mean, which would indicate there was no direction tuning at all (then F = 1).

In the right graph of Fig. 3.9 we see that the broadness of tuning is about the same for fanning and translation. This was somewhat surprising since fanning stimuli contain more translation directions than pure unidirectional translation stimuli. For example, a fanning stimulus close to the optimal direction may still contain a translation component which is in the preferred direction for a neuron which would be purely tuned for one single

direction Apparently, these 'secondary' translation components did not have much effect on the broadness of tuning However, exceptions were found (see Fig 3 7) Hence the similarity in broadness of tuning for translation and fanning stimuli is compatible with the idea that the tuning for fanning stimuli is primarily determined by the responsiveness to the main translation components (in the preferred direction) present in these stimuli Considering the population as a whole it is clear that there were no neurons sharply peaked for translation or fanning only The fact that a translation component within a fanning stimulus is broadly represented does hardly affect the broadness of tuning for fanning

Responses to real textured boards

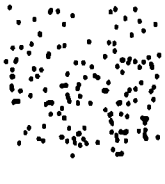
Finally, it should be mentioned that on 3 occasions, neurons responsive to fanning were also tested qualitatively with real boards rotating in depth during visual fixation In all cases, these neurons responded vigorously to such stimuli, provided that the axis of rotation and the position within the field were chosen appropriately In Fig 3 10 the maximum responses to artificial stimuli (A) and to a real textured board (B) were compared for a series of trials on a single neuron (N_7) Although the hand-held stimuli could not be controlled as rigorously as the fanning, it was striking that very crisp responses could be obtained with these primitive stimuli

The responses were evaluated with a shifted bin of 66 4 msec (4 frames on the HP stimulus computer) The bin with the maximum number of spikes was taken as the peak The stimuli used in both experiments were translation and fanning (rotation in depth) in the preferred direction The maximum responses to artificial stimuli were about as strong as to the real ones, although the former stimuli lacked cues based on disparity, deformation and local expansion/contraction of texture Note that the artificial fanning stimuli also lacked the change of the flow field parameters which occur in the case of tilting a real textured board This result suggests that the computer generated stimuli are comparable to real textured boards

3.4 Discussion

Rotation in depth

The main result of this chapter is that neurons in VIP appear to be sensitive to rotation in depth both for real planes and for 2-D "projected" planes rotating in depth ("fanning") VIP neurons, responsive to fanning, could be involved in the detection of planes rotating in depth (around an axis orthogonal to the visual axis) The question arises whether such sensitivity is newly created in VIP, or whether it depends on input from MST In MST, both Saito et al (1986) and Sakata et al (1986) encountered neurons which were responsive to the rotation of real objects (such as flat boards) in depth (Rd, Rotation in Depth neurons) It is possible that most of the presently described VIP neurons, exhibiting sensitivity to fanning, receive input from such MST neurons described by Saito et al (1986) and Sakata et al (1986) Support for this suggestion comes from the



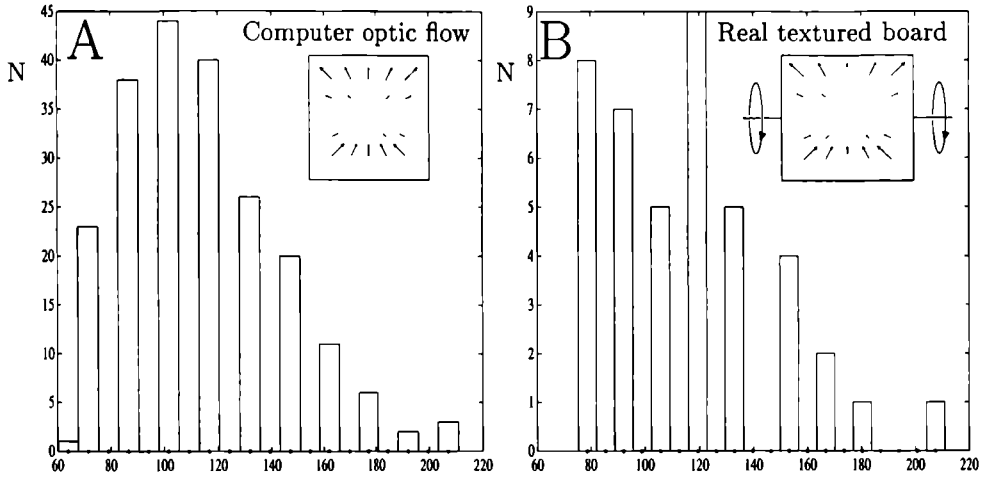


Figure 3.10: *Comparison of responses of a VIP neuron N_7 to computer generated fanning stimuli (A) and a real textured board (B). The maximum responses measured with artificial fanning produced by the HP computer (A) and with textured board held before the monkey (B) were determined using a sliding bin method. The latter method eliminates the chance of taking a lower maximum response because of taking a less optimal position of the bin with respect to the response peak. Bin width: 66.4 msec (4 frames on HP stimulus computer). Note that the real stimuli with the textured boards are less well defined for shape, movement direction, speed, timing etc. Also the number of trials is less. This explains the less regular shape of the distribution in plot B and the relatively larger fraction of smaller maxima's.*

observation that VIP neurons closely resemble MST neurons for other RF sensitivities as well, such as for divergence and rotation (this chapter, chapter 2 and Graf et al., 1995). On the other hand, the MST neurons described by Saito et al. (1986) and Sakata et al. (1986) may have been more specialized than the presently described VIP neurons, since they appeared to respond exclusively to rotation in depth while the neurons presented here, had a broader sensitivity and also responded to other basic optic flow components. This discrepancy, however, could be explained on the basis of differences in method. With textured boards it was not always clear as to which features contributed to the responses. Besides the optic flow, real planes have many other cues as to their shape and movement. The deformation of contours yields information for movement as has been shown by Rogers and Rogers (1992). The texture gradient is an important cue as well (Young et al., 1993). In the present experiments, such cues have been minimized in order to be able to evaluate the effect of the optic flow separately. To minimize the contour deformation cue, stimuli with a constant field of view were used. To minimize the

texture gradient, the dots had a finite lifetime, and their size was kept constant Hence, the only cues remaining were the speed gradient and the motion pattern (direction of the flow) The speed cue is not likely to be very important In MST most optic flow sensitive neurons are quite insensitive to the speed gradient in diverging stimuli and to the inward acceleration in rotating stimuli (Tanaka et al , 1989) This aspect has not been studied in such great detail in VIP Nevertheless, it was shown elsewhere that VIP responses to expansion/contraction closely resemble those observed in MST for many characteristics, including insensitivity to variations in speed and dot size, position invariance etc (chapter 2) A plane, rotating in depth, has edges which near each other when the plane approaches a position where it is parallel with the line of sight By using rotating drums, Saito et al (1986) could exclude that this was an essential cue But other questions were unsolved in their experimental set-up For example, both the dot size and the density of the structured patterns are bound to change both for rotating planes and drums, thereby causing contrast gradients Hence, it remains to be shown whether MST neurons can respond to the optic flow components of planes, rotating in depth, or whether they react to a different cue Secondly, the finding of specialized Rd neurons in MST but not in VIP may be due to real objects providing a much richer and stronger visual input than the more abstract, screen projected patterns The methods used by Saito et al (1986) were very different from the ones presented here, in that they did not use computer guided photic stimulation The latter type of stimulation may be generally less effective because of the (deliberate) exclusion of other important visual cues, such as changes in dot size or density In this respect it is important that some VIP neurons were presently tested with real stimuli as well The responses were not significantly different from those to artificially induced fanning, making it unlikely that sampling bias was introduced through differences in saliency of stimulation It should be pointed out that the present sample was relatively small, and this leaves open the possibility that there exist neurons with a higher degree of selectivity for rotation in depth, which were missed in this set of experiments Rd neurons constitute only a small minority of the neurons in MST In a more recent study of MST, Tanaka and Saito (1989) failed to find rotation-in-depth neurons and they ascribed this deficit to the dense clustering of these units in a small subsection of MST Most of the presently described neurons with sensitivity to fanning were found in an area of 2 by 2 mm of VIP in both hemispheres but there was no evidence for clustering of these neurons in VIP

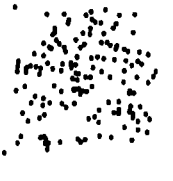
Mechanism of fanning sensitivity

All fanning sensitive neurons could be driven by translating dot patterns Furthermore the optimum fanning direction was almost always well predicted by the preferred direction of translation In such cases the optimal axis for the fanning could usually be correctly predicted to be the preferred direction for translation (Fig 3 3, $\phi_0 = -106\,9° \pm 3\,2°$ for translation and $\phi_0 = -94\,6° \pm 7\,4°$ for fanning) Nevertheless, for some of these neurons the responses to optimal fanning were larger than those to optimum translation, indicating that factors other than translation contributed to the overall fanning response For example, a small amount of sensitivity to rotation or divergence was sometimes

present along with a direction selectivity for translation In such cases the responses to fanning could result from the summation of the responses to both local translation and the other components The overlap between the regions yielding the largest responses either to fanning or to divergence can be understood by assuming that the responses to fanning were largely due to the local sensitivity to divergence In the group of 30 neurons tested for fanning, 13 could be classified as expansion selective (including spiral neurons with expansion) on the basis of their optimal response All but two of these 13 expansion neurons responded well to fanning since the responses to the latter stimuli were within 50 percent of the responses to divergence/rotation In the expansion sensitive neurons no evidence was found for the presence of adjacent receptive field regions sensitive to contraction It has been proposed that neurons, responsive to rotation in depth, could have combined sensitivity to expansion and contraction (Saito et al , 1986)

For neurons with small RF ("MT-like VIP neurons") it was found that the positioning of the center of the stimulus with respect to the center of the RF was very important for the responsiveness to fanning or first order optic flow This is similar to the observations of Lagae et al (1994) on stimulation of MT neurons with divergence/rotation type stimulation In MT-like VIP neurons, responses to fanning are mainly found after appropriate positioning of the stimulation (Fig 3 6) This suggests that such fanning responses are mostly due to the placement of the expanding part of the fanning pattern over the local maximum in divergence sensitivity

Amongst the fanning sensitive neurons with large RF, some neurons responded optimally to combinations of optic flow components (e g spiral neurons, as described by Graziano et al , 1994) In such cases it was often difficult to understand the underlying mechanism for the fanning response Using translating stimuli over subsections of the RF it appeared that the neurons were not equally sensitive throughout the whole receptive field Furthermore it was found that the subregions of the RF had mostly the same direction selectivity as the whole RF (see Fig 3 5) Hence local variations in preferred direction selectivity for translation are not at the basis of the sensitivity to either fanning or first order optic flow components In general it can be concluded that a fanning stimulus, simulating rotation of a plane in 3-D, activates many VIP neurons, presumably because of their underlying sensitivity to translation in a given direction and/or to first order optic flow The precise mechanism involved is certainly to be more complicated than a "mosaic" arrangement of subregions with different direction selectivities (in agreement with the analysis of Duffy and Wurtz, 1991b) Further experiments are needed to shed light on this issue



Chapter 4

Minimum stimulus duration for ON and OFF responses

4.1 Introduction

The 2-D optic flow projection on our retina contains important information about ego-motion A crucial question is how long such optic flow patterns have to be presented to be effective in our decisions about the direction we are moving For example, when one looks outside the car and then redirect its gaze on the road, how long does one need to look to appropriately judge the movement and speed of the car with respect to the environment?

Judgments of this kind rely on the capability of the visual system to analyze retinal optic flow Such flow can consist of simple translations but in most cases other basic components such as divergence, curl and shear will be present as well (Koenderink and van Doorn, 1975). The detection of these more complex optic flow components may be expected to be more difficult De Bruyn and Orban (1990) found that for the detection of translation, 4% of the dots in a random dot display had to show correlated movement, while this was about 10% for the detection of rotation, divergence and shearing One might also expect that the visual system requires more processing time for the analysis of higher order optic flow While translation can be detected in two frame stimuli, De Bruyn and Orban (1993) found that three frames at 35 Hz was the minimum number required for a nearly perfect (> 95% correct) identification of radial versus rotational flow fields This corresponded to a total duration of 85 ms Morrone et al (1995) used

Adapted from S J Schaafsma and J Duysens, Minimum stimulus duration for responses to optic patterns in the ventral intraparietal area Vision Research, submitted
and J Duysens, S J Schaafsma and G A Orban, Cortical OFF response tuning for stimulus duration Vision Research Vol 36, 1996, pages 3243-3251

longer stimuli (4 frames of 80 ms) for similar tasks but they did not report the lower limit needed

The processing of information about visual motion is thought to occur in several stages (Hildreth, 1984) At the lowest level, the detection of local motion occurs (bilocal motion detectors) The resulting signals are combined for the detection of more complex moving patterns presumably through cells with integrating properties (see Fredericksen et al , 1994) This view is consistent with the idea of Van Doorn and Koenderink (1985) that integration over several samples is needed for the perception of coherent motion

Amongst the various kinds of coherent motion it is well-known that translation is the optimal stimulus for area MT, while more complex optic flow patterns related to egomotion can be analyzed by parietal neurons which receive input from MT Neurons in MST are especially sensitive to expansion/contraction or rotation stimuli or to a combination of them (e g spiral stimuli, Tanaka et al , 1986, Duffy and Wurtz, 1991, Orban et al , 1992, Graziano et al , 1994, also area 7A, Steinmetz et al , 1987) Area MST provides input to still higher regions such as VIP, where cells respond well to optic flow stimuli (Chapter 2 and 3) Hierarchically speaking, VIP is at the end of a cortical line leading to neurons which can detect the visual consequences of egomotion and combine this information with somatosensory information about movement of (or on) the body In view of the psychophysical results mentioned it would be of interest to know how long the optic flow stimuli have to last in order to evoke discharges in these VIP neurons and to compare this with presentations of translations

A second related set of questions concerns the issue of what response parameters the brain possibly uses to make decisions about optic flow detection Is the relevant part of the response the maximum rate of firing or the average number of spikes? Is the relevant information stored in early phasic parts of the responses or are later tonic parts important as well? In MST, Duffy and Wurtz (1997b) distinguished between an early response (60-100 ms latency) and a tonic response (latency $>$ 100 ms) They found that tonic responses are more specifically related to optic flow stimuli than early responses Since VIP receives input from MST this raises the question whether these two types of responses are present in VIP as well and whether these components are able to convey direction selectivity even for stimuli of short durations For visual identification tasks in monkeys for example, selective responses to faces can occur with short latencies (about 70 msec for the most effective stimuli, up to 213 msec for slower neurons, Perret et al , 1982, Oram and Perret, 1992) but it unclear whether such responses do indeed contribute to behavioral recognition

Recently, it has become feasible to compare the psychophysical performance of monkeys with the neuronal discharges in visual areas which were thought to be involved in the corresponding tasks on discrimination of the direction of motion (Britten et al , 1992, Celebrini and Newsome, 1994) So far such studies have not investigated the question of minimum duration of optic flow stimulation However, several observations were made which are relevant to the present issue For example, Britten et al (1992) investigated the discrimination of weak motion signals in a stochastic visual display and found that both humans and monkey improved their psychophysical performance when viewing time was increased up to 2 seconds In parallel it was found that the neuronal threshold de-

creased over this same time period This raises the question as to what the role is of the tonic part of the neuronal responses Does this part contain information about direction selectivity?

To answer these questions, single unit recordings were made in area VIP of the awake monkey The aim of the present study was to correlate the available psychophysical data on humans with recordings from monkey VIP following stimulation with basic optic flow components (as used by others in area MST and VIP, see Tanaka et al , 1986, Duffy and Wurtz, 1991, Duhamel et al , 1991, Orban et al , 1992, Colby et al , 1993b, Graziano et al , 1994, Schaafsma et al , 1996) What is the minimum duration of stimulation required to elicit responses and over which range is there a response increment? If these neurons are at the basis of decisions about the detection of these components then one might expect that they require about the same amount of temporal integration as needed for the perceptual detection In principle it is possible that such cells exhibit a duration threshold behavior (where duration thresholds are the period a stimulus needs to be shown to be detected correctly, which we expect be in the same order as the related psychophysical thresholds) Alternatively, the cells could have a low duration threshold but somehow maintain direction sensitive information through tonic discharges To test these possibilities, the minimum duration of stimulation with optic flow components was determined for both phasic and tonic response components

Off response tuning for stimulus duration

The minimum duration of stimulation can not only have a pronounced effect on the phasic and tonic ON responses (as presented in this chapter) but also on the OFF responses

In the sample of VIP neurons in this thesis, OFF responses were encountered infrequently (see chapter on oscillatory stimuli) Therefore, an older set of data, obtained in areas 17 and 18 of the cat was used to answer the question on the duration sensitivity of OFF responses The results of this part of the study will be briefly discussed at the end of this chapter

To answer the question whether OFF response amplitude (firing rate) of visual cortical cells varies as a function of stimulus duration, an experiment was done in areas 17 and 18 of the cat The anaesthetized (Alfatesin for initial surgical procedures, curarized with a continuous perfusion of Flaxedil at 5 mg/kg/hr with D-tubocurarine added at 0 14 mg/kg/hr, and pentobarbitone intravenously at 0 2-1 mg/kg/hr) were quantitatively tested with handheld stimuli to determine the optimal stimulus dimensions (length, width, orientation of bar) The optimal stimulus (usually a light bar of 0 3 deg width with a luminance of 3 43 cd/m^2 against a background luminance of 0 05 or 0 65 cd/m^2) was rear projected on a translucent screen, and was flashed or moved over a speed range from 0 5 to 900 deg/sec over the receptive field A group of 58 cells were found for which the OFF responses varied as a function of ON stimulus duration Most cells (52) showed only a response increase with longer durations but 6 simple cells were tuned for durations between 50 and 400 ms For some of these cells this tuning could be used to predict adequately the velocity tuning

4.2 Methods

The preparation, stimuli, experimental paradigm, recording technique and off-line analysis were the same as described in chapter 2. After testing the neurons for their responses to translation, divergence, rotation and spiral stimuli a duration test was done, primarily for the most optimal stimulus, but in a few cases non-optimal stimuli were tested as well. Additional analysis was done as described below.

Off-line analysis

All trials during which the fixation was insufficient, were rejected. In most of the rejected trials the monkey started to fixate one of the moving dots, or was not fixating at the onset of the random dot stimulus. The selected responses to the repeated stimuli were averaged and PSTHs (peri-stimulus time histograms) were constructed. First the MFR (maximum firing rate; highest spike count in a single bin) was calculated. This was done by calculating all possible bins (sliding bin technique) For every spike a bin (33.2 ms) was constructed, ending at, and including this spike. This resulted in a set of bins which could overlap. The maximum bin in this set was taken as the MFR Using this method the determination of the MFR is independent of the positioning of the bins since all possible bin values are taken into account. Second the AFR was calculated. As for calculating the MFR, all possible bins (sliding bin technique) were calculated for the period from 500 ms before stimulus onset to stimulus onset. By taking the mean (further called mean bin rest activity) and standard deviation from the responses in these bins, an estimate was obtained of background activity and variability of the bin set. The response onset latency was then calculated from the first bin that was higher than this mean plus three standard deviations (a two SD criterion showed to be more noise sensitive, a four SD level showed comparable but slightly higher latencies). The offset latency was calculated

Figure 4.1: *Responses of a divergence neuron (D3.1) to a divergence stimulus of different duration. The dotted vertical lines indicate the period in which the response was analyzed. The other vertical lines (.−.) indicate stimulus on- and offset. The horizontal dotted line corresponds to the three sigma level above the average bin before stimulus onset (mean bin rest response, see methods). This level was used to determine the on- and off-latency of the response and thereby the period over which the AFR was calculated. The first bin crossing this level is shown for the on-latency. The other bins in the histogram were shifted with respect to this "threshold" bin. The binwidth used is 33.2 msec (corresponding to the duration of 2 frames). The lowest histogram shows the absence of response to convergence (npd, non preferred direction). Note that the data in the PSTHs is plotted based on the first bin corresponding to the onset latency. In all figures the positioning of the PSTHs is aligned to the first bin corresponding to the stimulus onset latency. Note that if the PSTHs shown would be based on the bin corresponding to the MFR they could be slightly shifted. Therefore, the maximum bin shown in the responses is most often not the MFR as calculated by the method described above, but slightly smaller.*

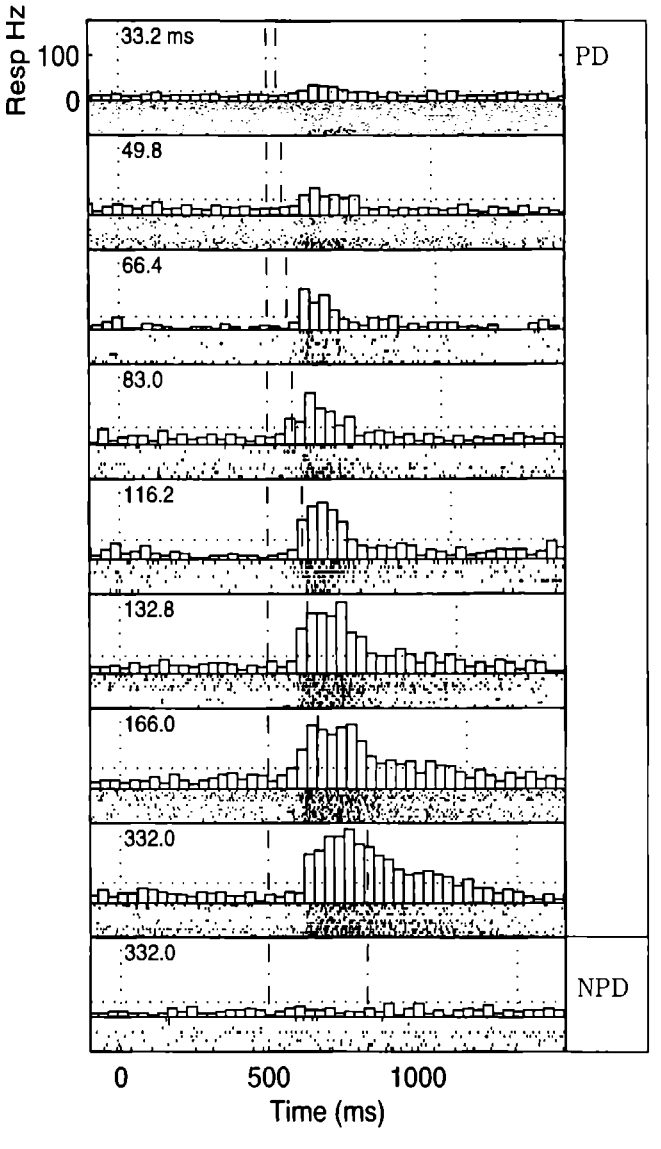

Resp Hz
100
0
33.2 ms
49.8
66.4
83.0
116.2
132.8
166.0
332.0
332.0
PD
NPD
0
500
1000
Time (ms)

Figure 4.1

from the first bin that was higher than this mean plus three standard deviations when going backward in time from 500 msec after stimulus offset (see vertical dotted line in Fig 4 1) The AFR (average firing rate) was taken as the average response between onset and offset latency

4.3 Results

Recordings were made of 161 neurons Among those neurons, 17 responded to smooth pursuit eye movements or saccades only and did not respond to visual stimulation In total 104 neurons gave significant responses to the moving light bar or a random dot flow field To perform the tests described in the present paper, a high degree of stability was required This explains why only 12 neurons could be tested quantitatively for their responses to the optimal stimulus for different durations

Duration test

In all cases studied, an increase in duration of stimulation yielded an increment in amplitude of responses In the example of Fig 4 1, repeated presentations of a divergent dot pattern induced only small but significant (above 3 SD of the background activity) average responses in an VIP neuron when only 2 frames were used (resulting in a stimulus duration of 33.2 ms) These responses had a latency of 98 ± 3 ms, which varied little with changes in stimulus duration The duration of the responses increased with stimulus duration At short durations of stimulation the responses occurred completely after the period of stimulation Nevertheless based on the constancy of the response latency, the responses were easily identified as being related to the onset of stimulation rather than to the offset The amplitude of the responses increased for stimulus durations up to 132 8 ms From Fig 4 1 it can be seen that stimuli in the non-preferred direction (NPD) were ineffective, and that the amplitude of the responses to stimuli in the preferred direction (PD) increased as a function of duration

The data, shown in Fig 4 1, were plotted for two response criteria in Fig 4 2, the MFR and AFR (see methods) for the different durations The maximum firing rate increased steeply up to a duration corresponding to 7 frames (132 8 ms) Both the MFR as AFR responses were fitted with the function $(m - b)(1 - \exp^{-\frac{a}{M-b}x}) + b$, where m corresponds to the maximum firing rate and $ax + b$ to the ascending slope for very short stimulation From the best-fitting curve through these data points, the dynamic range was determined as the range over which changes in duration were effective in inducing changes in response amplitude The measurement of this range was limited at the lower end by the minimum duration which could be tested (i e 2 frames or 33 2 ms) By intersecting the fitted response curve with the three-sigma above mean bin rest activity, an estimate was obtained of the low end of the dynamic range and thus the moment a significant response could be elicited At the higher end the dynamic range was limited by the point at which 80 % of the saturation level was reached For the example of Fig 4 1, the dynamic range for the MFR was 34-120 ms When instead the responses

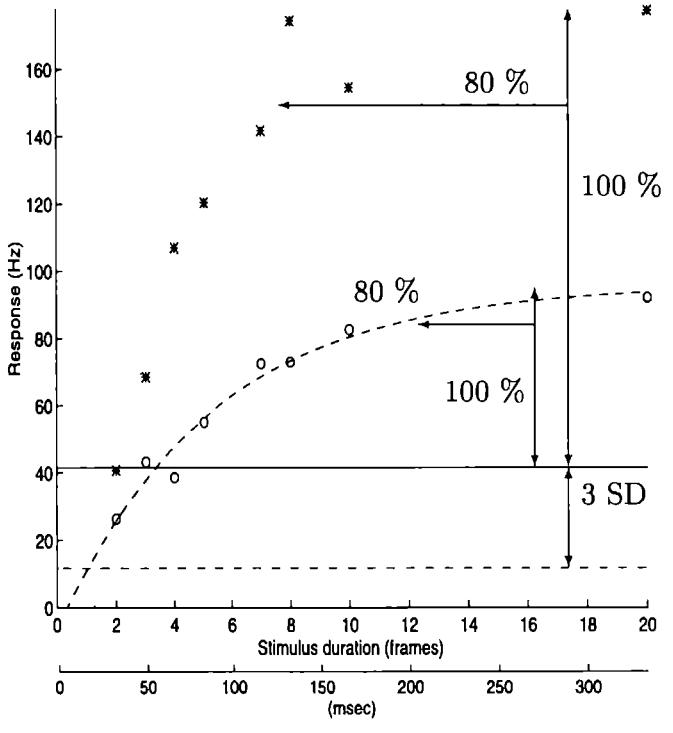


Figure 4.2: *Example of a fit trough the maximum response (MFR, *) and the average response (AFR, o) between the three-sigma crossings (neuron D3.1, divergence stimulus). The mean bin rest response (. – .) and the three-sigma above mean bin rest activity (—) are shown by the two horizontal lines. The data is fitted with the function* $(m - b)(1 - \exp^{-\frac{a}{M-b}x}) + b$, *where m corresponds to the maximum firing rate and* $ax + b$ *to the ascending slope for very short stimulation. The 100 % saturation response level (corresponding to m) and the 80 % (corresponding to 4/5 of the level of the three-sigma above mean rest activity to m) dynamic range levels are indicted for both the MFR as AFR.*

were measured in average firing rate then the rise in amplitude of the responses was less steep and the dynamic range was about 50 percent broader (54-188 ms).

Dynamic range of the neuron population

All neurons investigated were analyzed in the same way as explained for Figs. 4.1 and 4.2 (see Fig. 4.3). First let us concentrate on the DR for the MFR. For neurons tested with translation the upper limit of the dynamic range varied between 28.4 and 67.0 ms (mean 46.3 ± 17.8 ms). For the neurons tested with divergence, this upper limit varied between

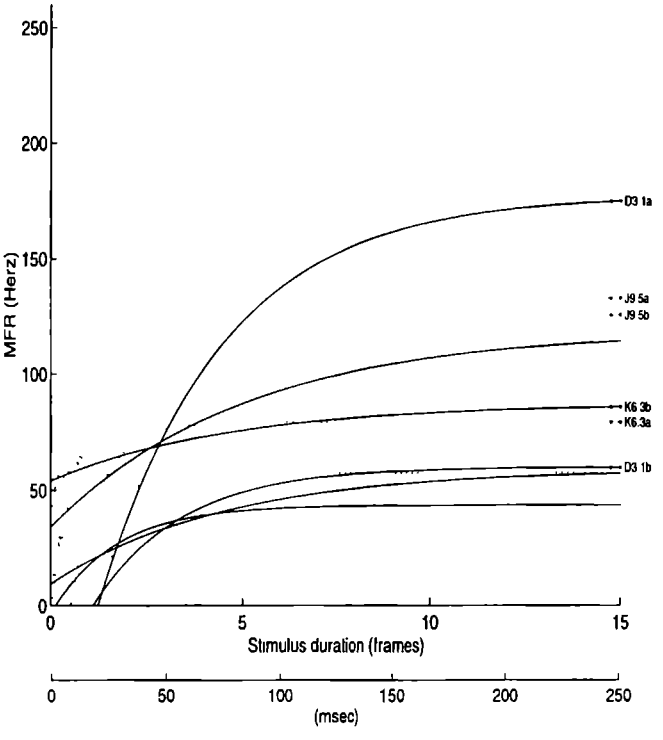


Figure 4.3: *Summary of duration tests on whole population. For each neuron, only the fit trough the maximum response (as in Fig. 4.2) is shown. Symbols: ... corresponds to translation and — to divergence. Three neurons (D3.1, J9.5 and K6.3) were tested both at optimal and sub-optimal speeds.*

70.0 and 195.5 ms (mean 118.1 ± 50.6 ms). In two cases the neurons could be tested for their duration sensitivity to two speeds of optic flow (Fig. 4.3). For these neurons (neuron J9.5 and D3.1 in Fig. 4.3) the stimulus was first presented at a suboptimal speed of 133°/s and later 267°/s. For the second neuron (D3.1), the optimal stimulus for divergence was shown at a speed of 100°/s while the non-optimal stimulus consisted of translation with the same mean speed. In both cases the use of non-optimal stimulation resulted in a lengthening of the dynamic range (upper limit changed from 29.7 ms and 120.5 ms for optimal stimulation to 84 7 ms and 196.0 ms for non-optimal stimulation, respectively).

Since sub-optimal stimuli can increase the dynamic range it may be argued that the broader dynamic ranges observed for neurons which respond preferentially to divergence as compared to translation may have been due to sub-optimal stimulation as well. To test this, the upper limit of the dynamic ranges were plotted in Fig. 4.4 as a function of

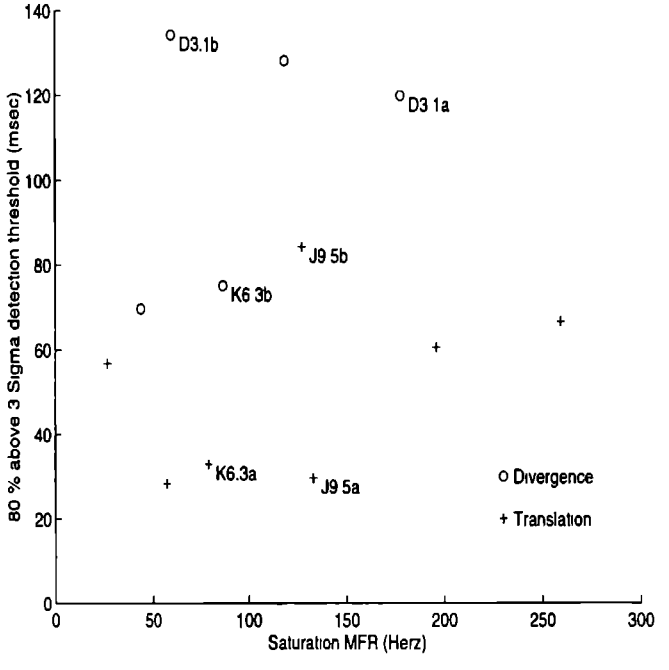


Figure 4.4: *A comparison was made between the saturation of the MFR and the latency of the duration threshold at 80 percent of the dynamic range. + corresponds to translation and o to divergence. Three neurons (D3.1, J9.5 and K6.3) were tested for both optimal and sub-optimal speeds.*

the saturation response level (MFR at a duration at which there was no further increase in response). It can be seen that the high upper limits of the dynamic ranges of the divergence neurons was not related to low response levels (low firing rates). In one case (neuron K6.3) the stimulation with divergence led to a higher upper DR (dynamic range) limit than for translation (33.0 ms for translation, 75.5 ms for divergence) but this can hardly be ascribed to a difference in response levels since the saturation MFR in that case was not significantly different for both stimuli.

Phasic versus tonic response components

In virtually all neurons the MFR was related to the early phasic part of the response. Hence by taking the MFR as response criterion the implicit assumption is made that duration dependency is coded primarily by the phasic part of the responses. To investigate the validity of this assumption some neurons were analyzed with AFR as response criterion as well (AFR measures the mean response over the whole stimulation period

and therefore is a combination of the phasic and the tonic response, see methods) An example is shown in Fig 4 5 This neuron exhibited a large phasic response for movement in the PD (preferred direction) and NPD (non-preferred direction) while the tonic response component was almost completely limited to movement in the PD Since the phasic response was expressed mainly in the MFR measure it is not surprising that the MFR response was about twice as large for movement in the PD as compared to the NPD The MFR response had a dynamic range (20 to 108 ms) which was compatible with the ranges found for the other VIP neurons The AFR response showed a similar increase in amplitude with duration but with a much broader dynamic range than for the MFR (145 to 611 ms, see Fig 4 6)

4.4 Discussion

VIP neurons represent the highest known level of processing of visual optic flow patterns potentially related to egomotion (Schaafsma and Duysens, 1996) The present study shows that such neurons in the awake monkey are able to respond to very brief (33 ms) two-frame presentations of optic flow patterns such as divergence One may recall that the detection of egomotion and heading is of vital importance for survival (consider the example of a pilot coming out of the fog in approach of a landing surface) Hence the visual system should be able to extract this type of information as fast as possible, even on the basis of short periods of stimulation

Many of the presently described VIP neurons responded to expanding flow fields and it has been speculated that these neurons may be involved in heading detection (Schaafsma and Duysens, 1996) The psychophysical data, indicating that very few frames are needed for the detection of heading, are consistent with the present finding that all VIP neurons tested, showed at least some response for two frame presentations of first order optic flow patterns Warren et al (1991) made psychophysical studies with random-dot displays that simulated translational and circular paths of movement They showed that the presentation of two frames (each 45 ms) was sufficient for 8 of the 12 subjects to determine accurately the heading direction provided the radial pattern of directions was preserved in the display For circular movement, observers required a 3-frame "direction field"

Dynamic range

Very short presentations of stimuli are not always sufficient to make accurate judgments, especially if the stimuli are complex or noisy In such cases one may expect that subjects rely on information provided by the response increments with duration (dynamic range)

In the study of Van den Berg (1992) the use of 2 frames was insufficient for the perception of relative movement of the subject with respect to the ground Furthermore the latter study indicated that the estimation of heading direction required point stimuli with a life time of at least 130 ms This is more than the 45 ms found by Warren et al (1991) He used pure translation (or movement along a circular path) while Van den

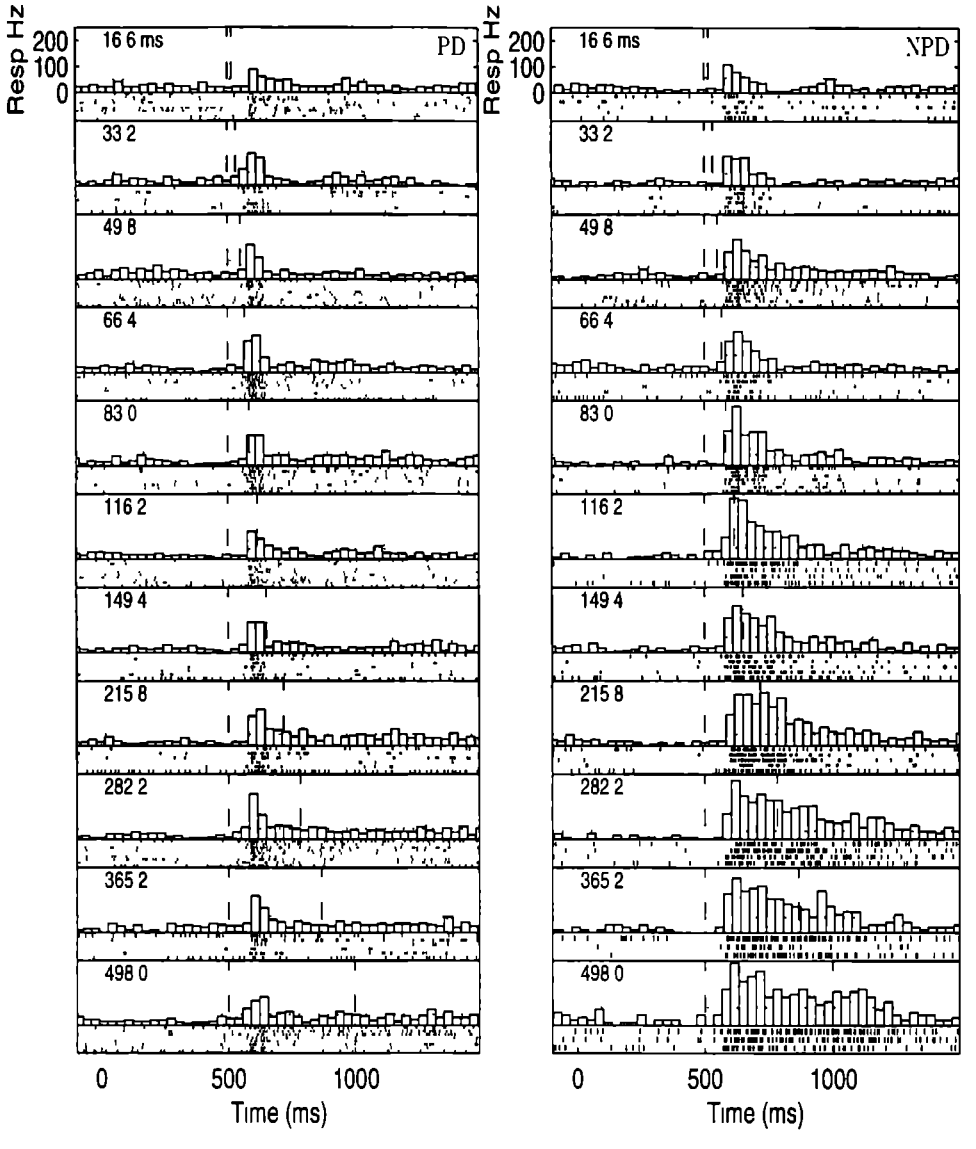


Figure 4 5 *Effect of stimulus duration on phasic and tonic response for preferred and non-preferred translation directions for neuron K3 4 Conventions as in Fig 4 1*

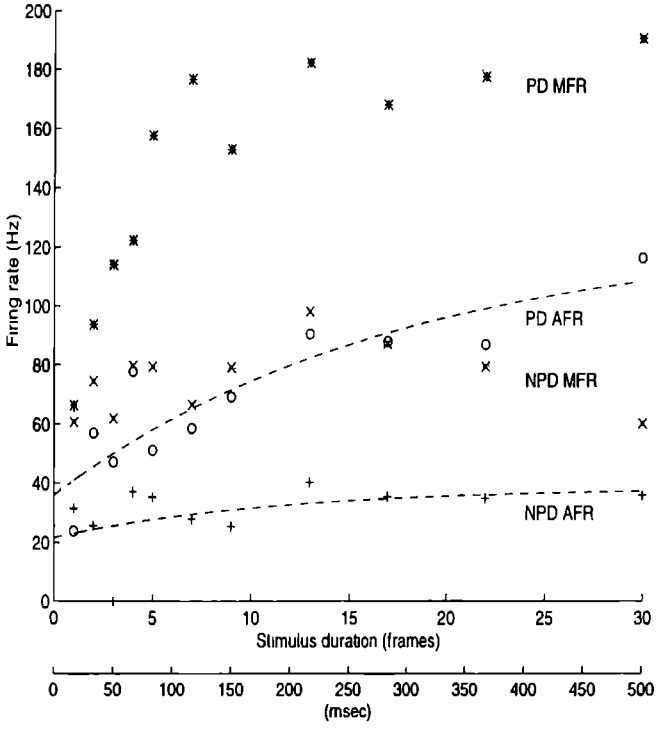


Figure 4.6: *Comparison of MFR and AFR responses of neuron K3.4 to translation in the preferred (PD) and non-preferred direction (NPD) at various stimulus durations.*

Berg (1992) used a combination of translation and rotation to simulate the movement.

For the neurons tested with divergence, the upper limit of the dynamic range over which a response increment was observed varied between 70 and 195.5 ms (mean 118.1 ± 50.6 ms). This is higher than the upper limit for neurons tested with translation (upper limit between 28.4 and 67.0 ms with a mean 46.3 ± 17.8 ms).

The broader dynamic range for divergence than for translation could indicate that detection of divergence could profit relatively more from duration increments than detection of translation. The available psychophysical data indicate that performance in translation detection tasks can also improve substantially when stimulus duration is increased, especially when the task is made more difficult than simple detection. De Bruyn and Orban (1988) found that discrimination of opposite directions was possible for the shortest duration tested (10 ms) while in discrimination tasks for direction and speed a strong dependency on duration was observed for stimuli lasting between 10 and 120 ms (see also Snowden and Braddick, 1991). For the correct detection and discrimination of velocity of translating stimuli McKee found that a minimum duration of 80-100 ms was

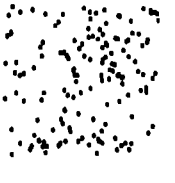
required (McKee and Welch, 1985) This duration depends on velocity (it is about 50 ms for 256 deg sec-1 versus 150-200 ms for 1 deg sec^{-1}, de Bruyn and Orban, 1993) Under noisy conditions it may take up to 400 ms for humans to discriminate motion speed or direction (Werkhoven et al , 1992) Even detection tasks are very duration dependent under such conditions For example, Grzywacz et al (1995) found that motion detection improves over durations extending to at least 600 ms

The recognition of structure-from-motion is another example of more complex analysis of motion signals requiring long processing times Treue et al (1991) found that recognition of a transparent rotating cylinder was nearly impossible for a viewing time of 100 ms and instead required about 400 ms

The increase in minimum stimulus duration with complexity of the task is also seen for other sensory modalities For example, Perrott et al (1993) studied the discrimination of moving events which accelerate or decelerate over the listening interval They found that the minimum duration required to discriminate between these two movement patterns was 310 and 90 ms, respectively, for displacements of 9 degrees and 18 degrees The accuracy of orienting saccades towards auditory targets is also strongly dependent on stimulus duration, especially with respect to elevation (Frens, 1995 pp 48)

Tonic responses

The present finding that tonic responses appear at long stimulus durations may help to understand that psychophysical performance improves with increment of visual exposure time and that postural responses appear only after relatively long exposures to optic flow (van Asten et al , 1988, Gielen and van Asten, 1990) In fact it was found that in some cases this tonic component was more direction selective than the phasic component at long stimulus durations (see Figs 4 5 and 4 6) and that direction selectivity kept increasing over a wider dynamic range for the tonic response criterion (AFR) The better selectivity of tonic versus phasic response components is in line with recent observations by Duffy and Wurtz (1997b) in MST The latter authors found that only about one-third of their cells had phasic responses which were direction selectivity while more than two-thirds of their cells had tonic direction selective responses In conclusion it is proposed that such tonic firing provides the animal or human with the necessary information to enable them to improve judgments about visual motion when stimulus duration is increased An alternative mechanism could be that neurons differ in the duration threshold at which they start responding This would be in analogy with area 17 cells having different duration thresholds for stationary visual stimuli (Duysens et al , 1985c) However, at present there is no evidence that cells in VIP differ with respect to their duration threshold for motion stimuli and therefore the present data do not support the notion that improved performance in motion detection is related to recruitments of novel motion detectors (with high duration thresholds) as stimulus duration is increased

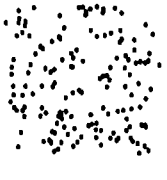


Off response tuning for stimulus duration

In cat visual cortex, many cells show ON responses which depend on the duration of presentation of a stationary bar (Duysens et al , 1985 a,b, Duysens et al, 1991), but a tuning for ON responses was not observed The study in this chapter shows that in this higher cortical area VIP a tuning for ON responses is lacking as well The responses reach a maximum while increasing the duration of stimulation

The main finding of Duysens et al (1996) was that OFF response amplitude of some cortical cells is tuned for the duration of the preceding ON stimulation Hence, there are two possible types of coding of visual stimulus duration The first relies on the duration of the ON response and the second on the firing rate following the period of stimulation (OFF response) The coding of stimulus duration by firing rate is not unique foi the visual system For sound stimuli, such frequency coding for stimulus duration has been reported in the frog's midbrain (Hall and Feng, 1986, Feng et al ,1990) and in the inferior colliculus of the brown bat (Eptesicus fuscus, Casseday et al ,1994) For the latter system, it was proposed that duration tuning arises in cells because of a combination of an early sustained inhibitory input and a delayed, transient excitatory input

Another interesting aspect is the relation between duration effects and the preferred velocity of a neuron In previous studies it was shown that the velocity characteristics of many cortical cells, stimulated with a moving light bar, can be predicted from a knowledge of the ON responses to stationary presentations of the same light bar for different durations (Duysens et al , 1985a) Some cortical cells however, give mostly OFF responses and for such cells it is more appropriate to try to predict the responses to a moving light bar on the basis of the OFF responses following ON stimulation of various durations The next chapter (chapter 5), suggests that interactions between ON and OFF responses can lead to enhanced selectivity for oscillation stimuli



Chapter 5

Responses to oscillations in VIP neurons

5.1 Introduction

Periodic motion abounds in everyday life, especially in relation to egomotion During body sway while standing, or during anterior-posterior head translations during walking, the retinal image oscillates Johansson (1973) has shown that the periodic motion of a few point lights on otherwise invisible persons is enough to recognize their specific way of locomotion (e g walking, running, dancing) In one of the experiments in his classic study, he shows that naive subjects are 100% correct when they view 10 point lights for only 1 sec, in which the invisible person makes about 1 step The question naturally arises if there is a neural correlate of this amazing capability, i e if there are neurons which are specifically sensitive to periodic motion Earlier studies have shown that there are neurons in V1, V2 and V4 that are specifically sensitive to spatially periodic patterns (Von der Heydt et al , 1992) In contrast, there are very few studies in which temporal oscillations have been studied in isolation and in these studies there was no comparison made with single translations (Gray and Regan, 1996) In the present study, a first step in that direction is made by looking for neurons which are sensitive to periodic motion, independent of spatial periodicity Furthermore, the visual stimulation is aimed at imitating motions which are important for egomotion (translation, expansion and contraction)

In the parietal cortex there are several areas which may play a role in the analysis of this type of motion The medial superior temporal area (MST) is thought to be involved in the perception of egomotion (Duffy and Wurtz, 1991a), and this area projects to the

Adapted from S J Schaafsma, T M H Dijkstra and J Duysens, Responses of neurons in the ventral intraparietal area of the awake monkey to temporal oscillations Journal of Neurophysiology, submitted

ventral intraparietal area (VIP) This latter area, which presumably is equivalent to the superior parietal occipital area (SPO) in humans (Tootell et al , 1996), may represent one of the highest placed areas in the chain of analysis of movement of our own body, or of objects moving towards us VIP is responsive to visual optic flow related to egomotion (Schaafsma and Duysens, 1996, Schaafsma et al , 1997), to vestibular input (Graf et al ,1996) and, in contrast to MST, also to somatosensory input (Duhamel et al , 1991, Colby et al , 1993b) Furthermore it is thought to receive extraretinal oculomotor signals (Colby et al , 1993b, Bremer et al , 1996) The hypothesis tested here, is that cells in area VIP are specifically sensitive to visual oscillations, since this area is thought to regulate body position in space and thus could be involved in the regulation of body sway

It is somewhat surprising that oscillatory stimuli have not been used systematically in neurophysiological laboratories When searching for visually responsive neurons it is customary to oscillate various types of visual stimuli across the receptive field However, for quantitative testing the motion of the stimuli is kept constant over time, mixed with pauses, and they are never presented as oscillating The reason why visual neuroscientists use oscillating stimuli during the initial search for responsive neurons is partly practical, because it is a method to repeat stimuli However, it may be that some neurons are selectively facilitated by this mode of stimulation For example, to explain direction selectivity of simple neurons in the visual cortex of the cat it was proposed that neurons with slightly offset receptive fields inhibit each other, and thus form a basic oscillating couple (Duysens et al , 1987) If such a scheme is correct, one would expect that oscillatory stimuli are particularly effective, since facilitation due to movement in the optimal direction could possibly add to the rebound excitation following the suppression which is due to the immediately preceding movement in the non-optimal direction Do such cumulative effects account for the apparent potency of perceived oscillations? A preliminary account of the results has been published (Schaafsma et al , 1995)

5.2 Methods

The preparation, stimuli, experimental paradigm, recording technique and off-line analysis were the same as described in chapter 2 Additionally, there were oscillation stimuli used as described below

Visual stimuli

The stimuli were generated by a graphics workstation and projected on a 2 x 2 5 meter (117° x 113°) translucent screen by a videoprojector at a 60 Hz frame rate The stimulus consisted of a random dot pattern of 40 dots of 4 7° diameter each Each dot had a lifetime of 332 msec For the constant speed trials the stimuli were shown repeatedly over the receptive field for periods of 1 1 or 1 5 sec in random order The individual trials were separated by 1 sec For the periodic trials, the stimuli were shown in oscillation with frequencies ranging from 0 2 to 6 Hz The oscillation was usually sinusoidal but occasionally triangular waves were used The triangular waves allow for better comparison

with the constant speed stimuli, but the sinusoidal waves relate better to a more natural stimulation The periodic trials have a length of 5, 15 or 20 cycles and contain 0, 2 or 4 phase perturbations where the phase shifts by 180° (See Fig 5 1C for a trial with 4 phase perturbations)

Off-line analysis

First, all trials during which the fixation was insufficient, were rejected Special attention was given to the occurrence of oscillating pursuit responses since some neurons showed pursuit related activity None of the neurons showed saccade related activity and therefore the fixation rejection criterion for saccades was lenient in some cases (but always after ensuring that saccades had no effects) The trials at the low frequencies (20 cycles at 0 25 Hz) could take well over a minute and it was unavoidable that the monkeys made a few small saccades In practice there never was a major problem since there were no instances in which the monkeys made systematic periodic saccades The selected responses to the repeated stimuli were averaged, and peri-stimulus time histograms (PSTHs) were constructed as shown in Fig 5 1

For the constant speed trials two response characteristics were calculated The amplitude of the responses was evaluated by measuring the maximum firing rate (MFR, the highest spike count in a single bin of length 33 msec), and the average firing rate (AFR, the average spike count during the trial) The MFR is a measure for the phasic part of the response, the AFR for the tonic part The optimal direction (OD) is defined as the direction in which the largest MFR occurred This was usually related to the phasic part of the responses (see results) Note that OD was not necessarily the direction in which the AFR was the highest (e g see Fig 5 1A,B)

In comparing constant speed with periodic stimuli, the data showed (1) that the mean firing rate averaged over OD and NOD tended to be the same, and (2) that the difference between the peak and valley of response for periodic stimuli tended to be larger than the difference in response for constant speed between OD and NOD Also the peak and valley of response for periodic stimulation did not always coincide with the stimulus movement in the OD and NOD In order to bring out the similarity in mean firing rate the mean of the AFR in the OD and NOD was compared with the mean of the AFR during oscillation In order to bring out the difference in responses to constant speed and periodic stimuli a *motion contrast* was used For the constant speed condition, this contrast was defined as $\mathrm{abs}((AFR_{od}-AFR_{nod})/(AFR_{od}+AFR_{nod}))$ with AFR_{od}, AFR_{nod} the AFR in the OD and NOD response For the oscillating condition, a determination was made which half of the stimulus cycle showed the maximal response, and during which cycle the response was minimal Subsequently the AFR during each of these halves as AFR_{opt} and AFR_{n-opt} was calculated Then the motion contrast was calculated as $(AFR_{opt}-AFR_{n-opt})/(AFR_{opt}+AFR_{n-opt})$ The contrast was generally calculated over all cycles except the first two, because the response to the first two had a lower contrast for many cells (see e g Fig 5 1)

The *onset latency* of the responses for both conditions was measured based on a comparison between the response and the background activity in the 500 ms period

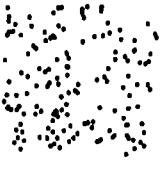
prior to the onset of stimulation. The point at which the response first crossed a level corresponding to three times the standard deviation of the background activity was taken as the onset latency. For the periodic motion stimuli, the phase relationship between stimulus velocity and response was quantified also. This was done by taking the time difference between the rising zero-crossing of velocity, and the peak of response, and dividing this difference by the period of the stimulus. The time of occurrence of the response peak was established by fitting a gaussian to the response profile (Levenberg-Marquardt nonlinear regression; Press et al, 1992), and taking the time of occurrence of the maximum of the fitted gaussian. As some response profiles were asymmetric, this procedure introduced some bias in the estimate of relative phase. However, the shifts in relative phase observed between the first response peak and subsequent ones, is much larger than this small bias. In order to compare the timing of the first response (that seems to have a fixed time delay) with the timing of subsequent responses (that seem to have a fixed phase delay) a gaussian was fitted to the first response both for the periodic and the constant speed stimuli. The latency of the peak of this gaussian relative to the start of stimulation is called the *peak latency*, and relates to the phasic response in the constant speed trials.

5.3 Results

Recordings were made of 178 neurons, from which 110 responded to moving visual stimuli. A total of 16 neurons were selected to be quantitatively tested with oscillating stimuli. For all these neurons it was checked whether there was a saccade and/or a smooth pursuit related response. None of the neurons discussed in this chapter showed a saccade related response. Seven neurons (J7.5, J8.1, J11.1, K3.4, K10.1, L0.1 and L4.1) showed a smooth pursuit related response. All 16 neurons were presented both with constant speed and with oscillating stimuli during periods of steady fixation. In all cases, including for the smooth pursuit types of neurons, the monkey was able to maintain its fixation despite the oscillations.

The responses to oscillating stimuli were compared to the responses to constant speed

Figure 5.1: *Responses of the neuron J10.5 to a translation with constant velocity in the optimal and non-optimal direction (100°/s) are shown in the two upper panels (A, B). In the lower three panels (C, complete and D,E, enlarged) the response to an alternation of the direction of translation (speed 100°/s) is shown (triangular modulation). For all trials the eye movement in the horizontal (EyeX) and vertical (EyeY) are shown in the two upper parts of the panel. The responses are shown both in the averaged histogram (33.2 ms bin) and for individual trials. The speed modulation of the translation stimulus is shown at the bottom. The scale of the displacement (x), speed modulation (v) and acceleration (a) profile are kept the same for all three panels. Stimulus on- and off-set are indicated by the dot-striped marker. The dotted lines indicates zero velocity. Note the four phase shifts to test the recovery time constant of the neuron.*



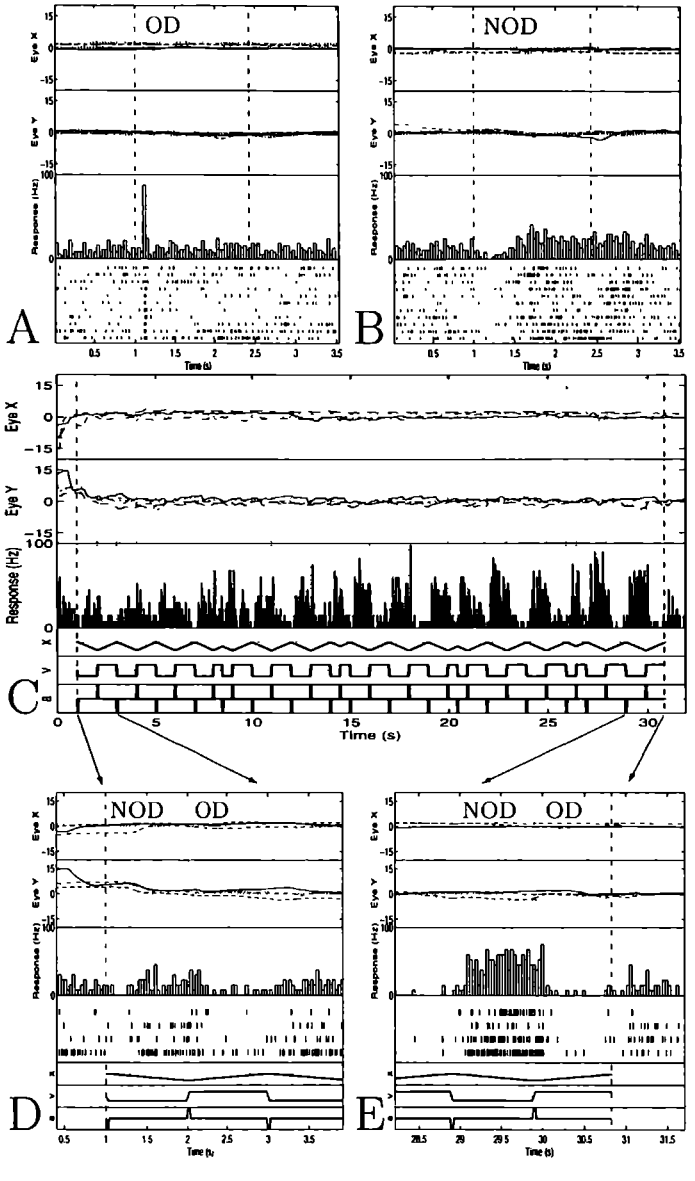


Figure 5.1

motion in the OD and NOD (optimum and non-optimum direction defined in terms of the largest MFR, see methods) This is illustrated in Fig 5 1 In response to constant speed translation, neuron J10 5 responded both with a phasic and a tonic component The phasic response in the OD was facilitatory (MFR=88 spikes/sec) and occurred with an onset latency of 97 msec (Fig 5 1A) In the NOD the phasic response was suppressive Furthermore, this neuron showed a tonic response (MFR=24 spikes/sec, measured from the onset of the tonic response to stimulus termination) which was more prominent for movement in the NOD and had an onset latency of 655 msec (Fig 5 1B) The average firing rate (tonic and phasic combined) was larger for movement in the NOD (AFR=17 spikes/sec) than in the OD (AFR=14 spikes/sec) The tonic response persisted after termination of the stimulus (second vertical line in Fig 5 1B)

The same translations were also presented as an oscillating stimulus with a frequency of 0 5 Hz during fixation (Fig 5 1C) Note that the response is phase-locked and the peak has an average phase delay of 137 degrees (760 msec time delay) relative to the onset of the NOD movement This phase delay was comparable to the one seen for the tonic responses in the single motion trials in the NOD (Fig 5 1B), where the mean peak delay was 720 msec In Fig 5 1D and E, the response during two oscillatory cycles at the beginning and end of stimulation is illustrated on the same time scale as the one used for the constant speed translations (Fig 5 1A,B) At the start of the oscillation (Fig 5 1D) movement is in the NOD, and there is a response profile similar to the constant speed trials the onset latency is 415 msec and the tonic response peak has an amplitude of 18 spikes/sec (from the tonic onset latency to NOD termination), similar to the tonic response for constant speed motion (24 spikes/sec) During oscillation (Fig 5 1D) a movement in the OD followed the NOD movement and the resulting response differed from the constant speed OD response Movement in the OD now resulted in the shortening of the tonic response of the NOD (compare Fig 5 1D with 5 1B) This response shortening is even more apparent after a few oscillation cycles (Fig 5 1E) Furthermore, the facilitatory responses prevailed in NOD and gradually increased At the end of the oscillation series the response was clearly larger than the tonic response to constant speed translations in the NOD (Fig 5 1B) During oscillations, the tonic response lasted until 124 msec after the beginning of the movement in the OD (Fig 5 1E), making it difficult to distinguish the phasic component for movement in the OD (Fig 5 1A) During most of the OD movement the neuron was silent, indicating a suppression of firing This "new" suppression in the OD stimuli during oscillation could not have been predicted by the response to constant speed stimuli in the OD (Fig 5 1A) The increase in both the tonic NOD and the suppressive OD response caused a sharpening in motion contrast which is defined as the absolute value of $(AFR_{opt} - AFR_{n-opt})/(AFR_{opt} + AFR_{n-opt})$ The motion contrast increased from 0 24 for the first cycle (Fig 5 1D) to 0 75 for the last cycle (Fig 5 1E) The motion contrast for the constant speed trials was 0 097 Since there was an increase both in the facilitatory and in the suppressive response, the average firing rate during oscillation (20 spikes/sec) was only slightly higher than the one seen for constant speed motion (16 spikes/sec)

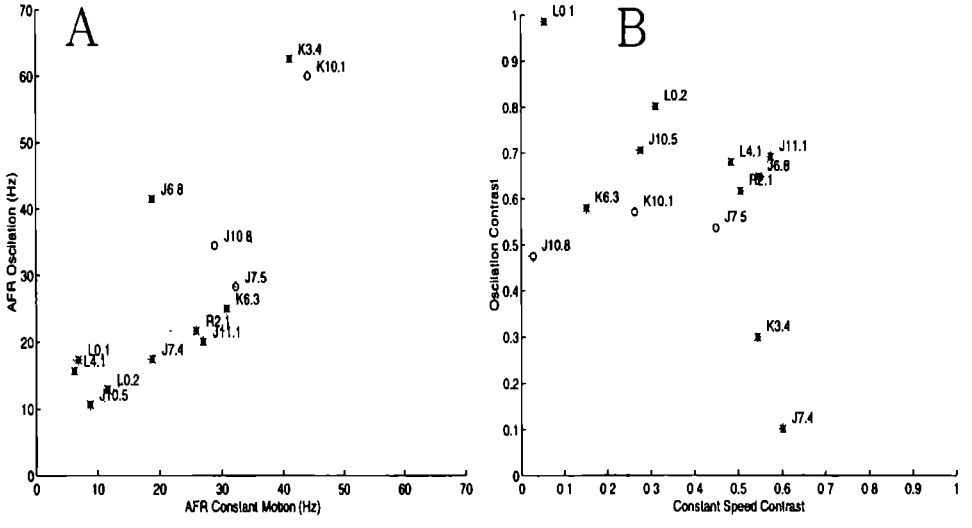


Figure 5.2: *Comparison between responses to sinusoidal oscillation and constant speed stimulation conditions. In panel A the mean of the AFR in OD and NOD is plotted against the average response during oscillation (alternating OD and NOD). In panel B the contrast for both conditions are shown. In both panels the dotted lines represent standard error (SE). The star-marked neurons were tested for translation, the circle marked for divergence. No constant speed trials were measured for neurons L0.3, D4.6 and J8.1 . Note that the data presented in this figure is based upon sinusoidal oscillation. Therefor, the data shown in Fig. 5.1 for neuron J10.5 is not the same since it is based upon triangular modulation at a speed of 100 deg/s.*

The amplitude of response

A comparison of amplitude of responses between the constant speed condition and the periodic motion condition for the whole population of 13 neurons (for 3 of the 16 there was not enough data for the constant speed condition) is shown in Fig. 5.2. In the left panel (Fig. 5.2A) it is seen that there is little difference in average firing rate between the two conditions (AFR, taken over all data). This is borne out in a paired t-test ($p = 0.1$ n.s.).

However, in the right panel (Fig. 5.2B) we observe that the motion contrast, as measured over all cycles except the first two, is larger for the periodic motion condition in the majority of neurons tested (11 out of 13). This difference is significant in a paired t-test ($p = 0.04$). Hence, these cells were more direction selective for oscillations than for constant speed stimuli. It explains why responses often appear much clearer for oscillating as compared to constant speed stimuli. In fact, in the total sample there was one neuron which was only identified because of the use of oscillating stimuli to

screen neurons (J10.5, Fig. 5.1). With the constant speed stimuli, the response of this neuron was so weak when compared to the background noise, that it was undetectable by ear. The two neurons (K3 4 and J7.4) which showed a lower motion contrast during oscillations lacked inhibitory responses in either OD or NOD during constant speed or oscillatory stimulation.

Triangular versus sinusoidal stimulation

Two types of oscillations were used, triangular (or saw-toothed, as in Fig. 5.1) and sinusoidal. Both yielded phase-locked responses with similar phase lags. The main difference was that a gradual build-up of response was seen for the triangular oscillations but not for the sinusoidal oscillations. This was found in all 5 neurons tested for the triangular oscillation while it was absent for sinusoidal stimuli in all of the 16 neurons tested. For the triangular trials the response of the third peak was always larger than the first (on average 1.5 times higher; SD=0 5). For the sinusoidal trials this average was 1.1 +/- 0.2, indicating an on average slight, but not significant increase in response during sinusoidal stimulation.

Both types of oscillation are repetitive but the major difference between the two is that the sinusoidal oscillations were predictable from the first three stimulus frames (50 msec). This follows from the following reasoning: let $x(t) = \sin(2\pi ft)$ be the position signal of the sinusoidal stimulus with frequency f then the acceleration follows by double differentiation as $a(t) = -(2\pi f)^2 \sin(2\pi ft)$ and one can calculate f by taking the ratio between the position and acceleration signal. Thus, assuming no noise in detection of the position signal, the monkey could extract the frequency of the stimulus in three frames, as three frames are necessary to calculate acceleration. Hence if the changes in response to oscillations were due to the predictability of the period of the stimulus and not to the repetition itself then there are differences between in the first cycles after stimulus onset. The findings are illustrated in Fig. 5.3 for neuron L0.2.

The responses to constant speed translations are shown in Fig. 5.3A,B. In many ways the responses were similar to the ones of the previously described neuron (Fig. 5.1). Movement in the OD elicited a phasic response while movement in the NOD caused a tonic discharge which persisted after the movement ceased. However, in contrast to the previous neuron, this neuron showed some suppression following the phasic response (Fig. 5.3A). During triangular oscillations the neuron showed phase-locked responses with a mean relative phase of 330 +/- 5 degrees. Furthermore, the amplitude of response increased over the first two cycles The response to sinusoidal stimulation showed similar

Figure 5.3: *A,B: Responses of the neuron L0.2 to translation in OD and NOD. Speed was 33.3°/s. C,D: Responses of the neuron L0.2 to an alternation of the direction of translation (max speed 66.7°/s). The responses are shown both in the averaged histogram (33.2 ms bin) and for individual trials. The speed modulation of the translation stimulus is shown at the bottom of each panel. In the panel C we see the responses to a stimulus with a triangular speed pattern, in panel D is the speed sinusoidally modulated.*

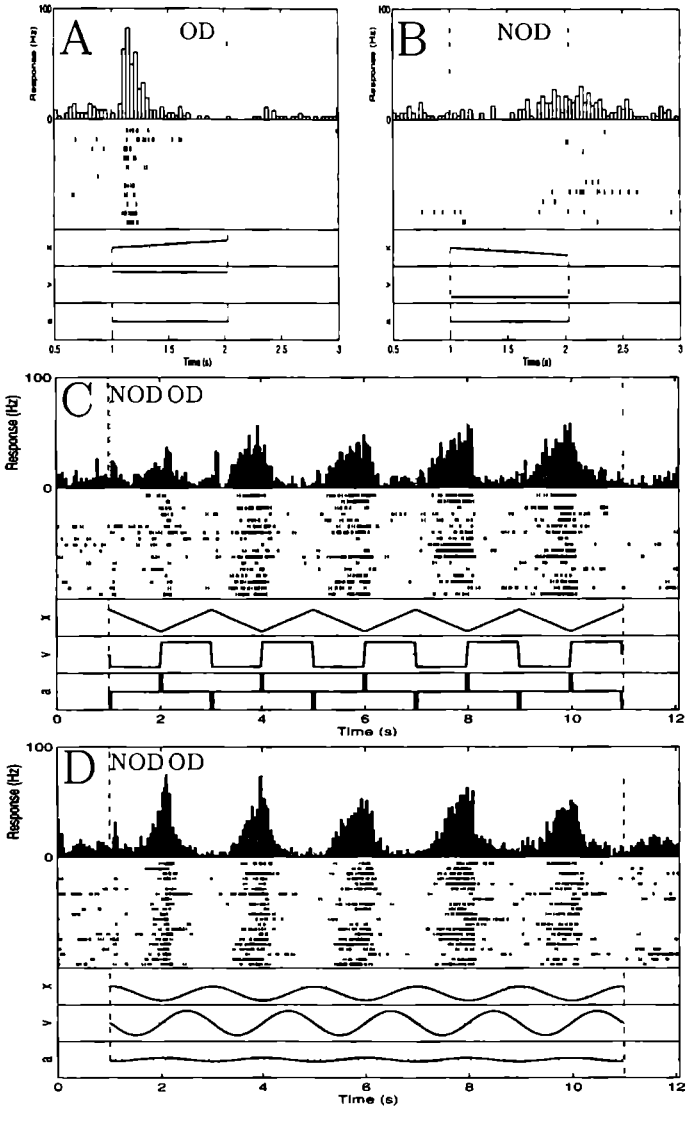


Figure 5 3

phase-locked responses with a mean relative phase of 342 +/- 4 degrees and with no increment in amplitude over the first 2 cycles

Note that for both types of oscillations the main part of the oscillation response

occurred in the NOD and the peak occurred prior to the onset of the OD. Hence for this cell the main response during oscillation cannot be related to the phasic response to translation in the OD. Instead, it is primarily the tonic response component seen in the translation NOD which increases during oscillations.

The timing of the responses was not significantly different for the triangular and sinusoidal type of stimuli. The main difference was in build-up of responses (found in all 5 neurons tested for the triangular oscillation), since the maximum response amplitude was present from the first cycle onwards for the sinusoidal stimulation. This absence of build-up for sinusoidal stimuli was seen in all of the 16 neurons tested.

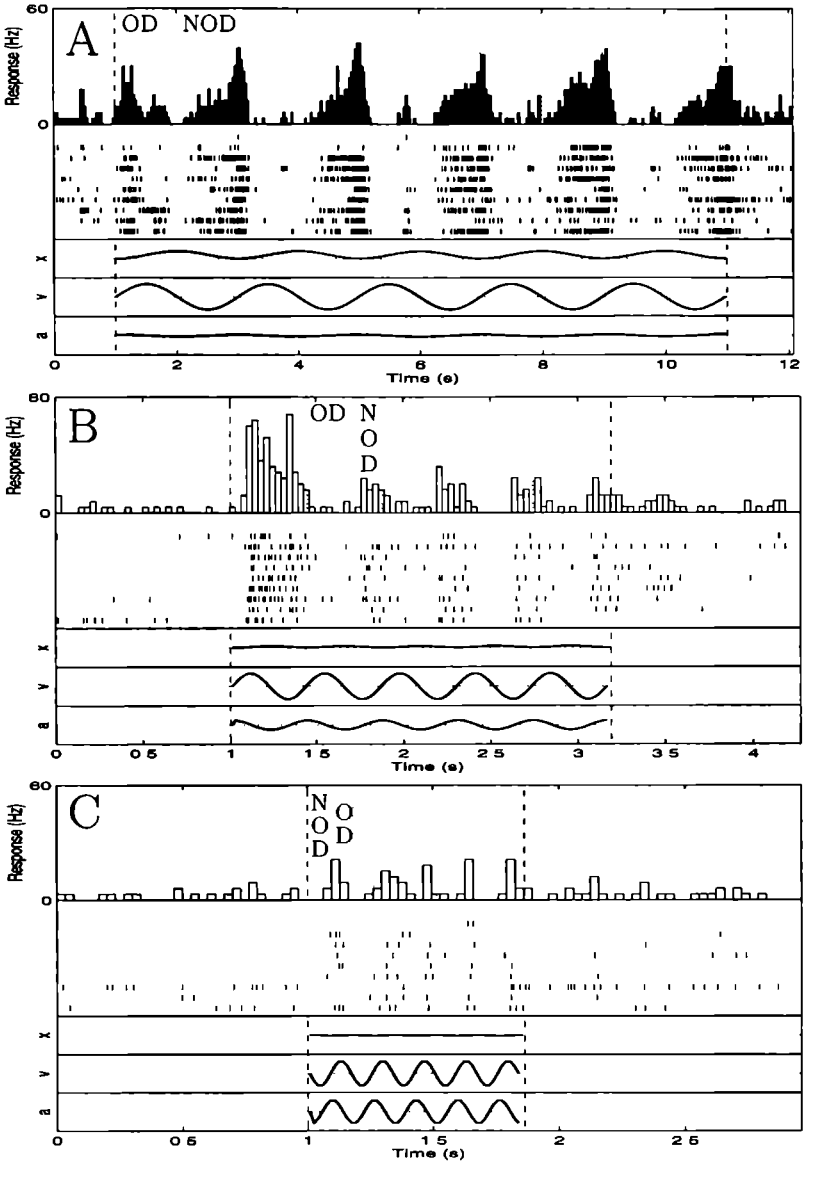
The timing of response

Phase-locking as seen in Fig. 5.3 were seen over a wide range of velocities and frequencies. For the cell of Fig. 5.3 the maximum amplitude of the responses varied from a maximum of tenths of spikes to a minimum of one spike for maximum speeds ranging from 150°/s down to 3.9°/s at a stimulus frequency of 0.33 Hz. Over which range of frequencies could cells respond with phase-locking? An example of the responses for different frequencies of a typical neuron is given in Fig. 5.4 for three frequencies (0.5, 2.3 and 6.0 Hz). This is the same neuron as plotted in Fig. 5.3. Phase-locked responses can be seen at the three frequencies. The amplitude of the responses was largest for the lowest frequency (0.5 Hz; Fig. 5.4A). At the highest frequency (6 Hz; Fig. 5.4C) the response consisted of one or two spikes for each cycle.

It is clear from the results presented so far that there are basically two types of responses. A phasic response which is limited to the first cycle and a tonic response which is seen for each cycle of the oscillation (Fig. 5.4). The nature of these responses is illustrated by their latencies. If a response is purely a stimulus-driven onset response, then it should have a fixed latency relative to the onset of stimulation irrespective of the cycle period. If it is related to the temporal characteristics of the cycle and not the onset one would expect that no fixed onset latency is found, but instead there should be a fixed phase relationship with the periodic stimulus. Phase-locking is then the result of period-related responses. Fig. 5.5 shows the result of this type of analysis.

A comparison was made between two response characteristics: the phasic response (first response peak after onset of stimulation) and the tonic, phase-locked response to sinusoidal stimulation. This was done at different frequencies (0 2 to 2.3 Hz) and different speeds (33, 67 and 133 deg/sec), all in the same neuron (L0.2) The result of this analysis is shown in Fig. 5.5. This plot illustrates the temporal and phase relationship between the

Figure 5.4: *Responses of the neuron L0.2 to sinusoidal oscillatory translations (max speed 133°/s) for different frequencies (0.5, 2.3 and 6.0 Hz). The responses are shown both in the averaged histogram (33.2 ms bin) and for individual trials. The speed modulation of the translation stimulus is shown at the bottom of each panel. The scale of the displacement (x), speed (v) and acceleration (a) profile are kept the same for all three panels. The dotted lines indicates zero.*


A
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0 2 4 6 8 10 12
Time (s)
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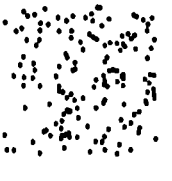
Figure 5.4



oscillatory stimulus and the phasic and tonic response peaks. When tested with different frequencies the neuron showed a phasic response with a constant peak latency of 177 +/- 7 msec following the onset of stimulation (Fig 5.5A). This resulted in a shifting phase relationship with the stimulus (Fig. 5 5B) The peak latency of the response did not vary with the speed of the optic flow. In contrast to the phasic response, the tonic response had a constant phase relationship with the stimulus. This is illustrated in Fig. 5.5D, where the relative phase of the second, third and fourth response peak relative to the rising zero-crossing of velocity is shown. The mean relative phase averaged across frequencies, speeds and response peaks, was 350 degrees, which means that the larger part of the response occurred during stimulation in the NOD (see also Fig. 5.3C,D).

The results of an analysis of timing across the population of 16 neurons is shown in Fig. 5.6. In this plot the relative positions of the response peaks (average over all peaks except the first two) are shown. One can distinguish two types of neurons. One group, shown at the top of the figure, represents neurons in which the timing of responses to periodic stimulation was predicted by the responses to constant speed stimulation. Hence all these neurons had the peak of their responses in the OD part of the oscillatory stimulus and more than 90 percent of their response was during the OD part of stimulation. None of the neurons in the first group showed a phasic response directly after the onset of the stimulus. Note that the peak of the response of the neurons in this group occurred near the peak velocity in the OD. For the second group, the responses to periodic stimulation were not well predicted by the responses to constant speed stimulation. As we will see later, even one neuron showed a reversal of preferred direction. The other nine neurons showed a response more or less evenly distributed around 360 degrees, the switch from

Figure 5 5: *Responses of neuron L0.2 to sinusoidal oscillatory translations (OD first as in Fig. 5.4A) at different frequencies for three speeds. The lines -.-, - - and — correspond to maximum speeds of 133.3, 66.7 and 33.3 degrees per second. In the upper right panels (A,B) the response characteristics of the first quarter of the phase (Phasic response), relative to time (A) and the phase (B) of stimulation are plotted. In the lower panels the peak time (C) and the relative phase (D) of the second, third and fourth phase repetition are plotted. Note that the latency of the phasic response (A) is not related the frequency of stimulation, except for a small effect, probably due to the average speed in the first three frames of stimulation which is higher at frequencies higher than 2.4 Hz, resulting in a slightly downward slope. The phasic response has a constant peak latency of 177 +/- 7 msec for the different frequencies tested. In contrast, the peak latency in the constant speed condition was 122 msec. The 55 msec difference in peak latency to the phasic response in the oscillating condition can be explained by the difference in velocity components of the two types of stimuli: constant velocity (33.3 deg/sec) for the single motion and sinusoidal variation (21 deg/sec for oscillations at 0.5 Hz and a maximum speed of 133.3 deg/sec after three frames) in the case of the oscillations. Note that no data was available for the lowest frequency (0.2 Hz) at 133.3 deg/sec. The data for higher frequencies could not be fitted with a gaussian and is therefore not included in this figure.*

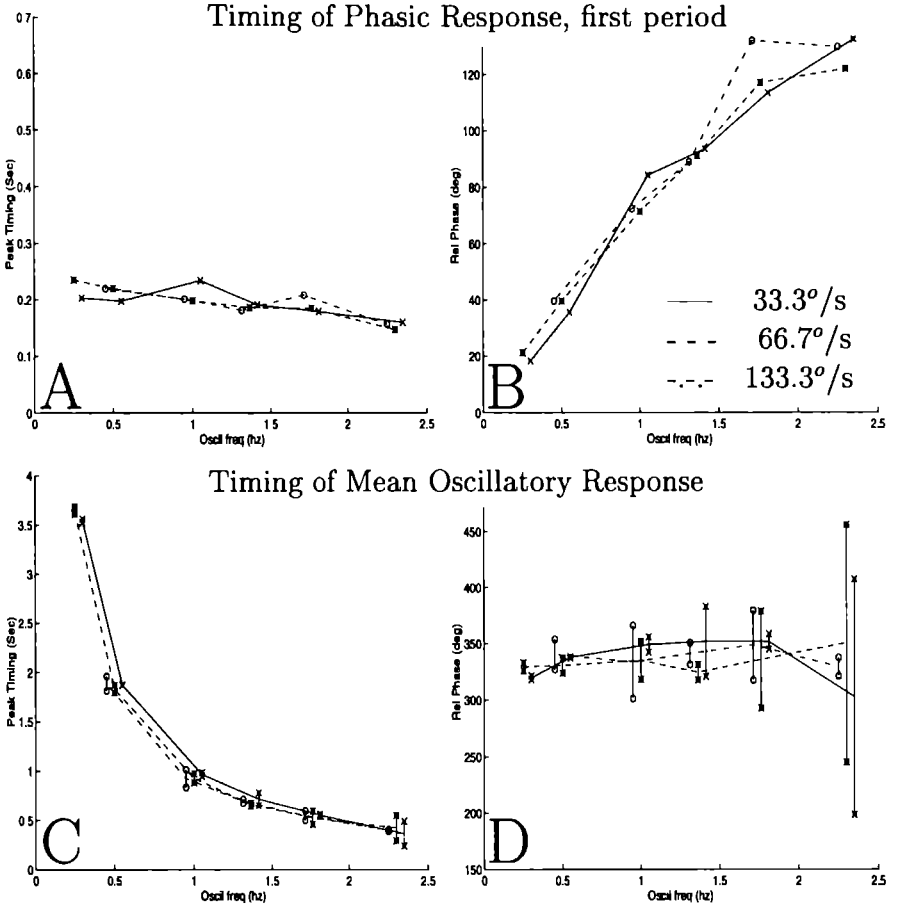


Figure 5.5

NOD to OD. For all neurons in this second group, the peak response around 360 degrees (the rising zero crossing of velocity) was higher than expected on the basis of the responses in the constant speed trials.

Examples of cells in the second group were already presented in Fig. 5.1 and 5.3. During oscillations the main responses started while the movement was in the NOD, and the peak occurred either in the NOD or early in the subsequent OD. A similar (tonic) response can be observed in the single motion trials (Fig. 5.1B, 5.3B) but during oscillations the total response of the peak is generally higher. The phasic response (Fig. 5.1A, 5.3A) is likely to contribute to this increase of response during oscillation (see below). As seen

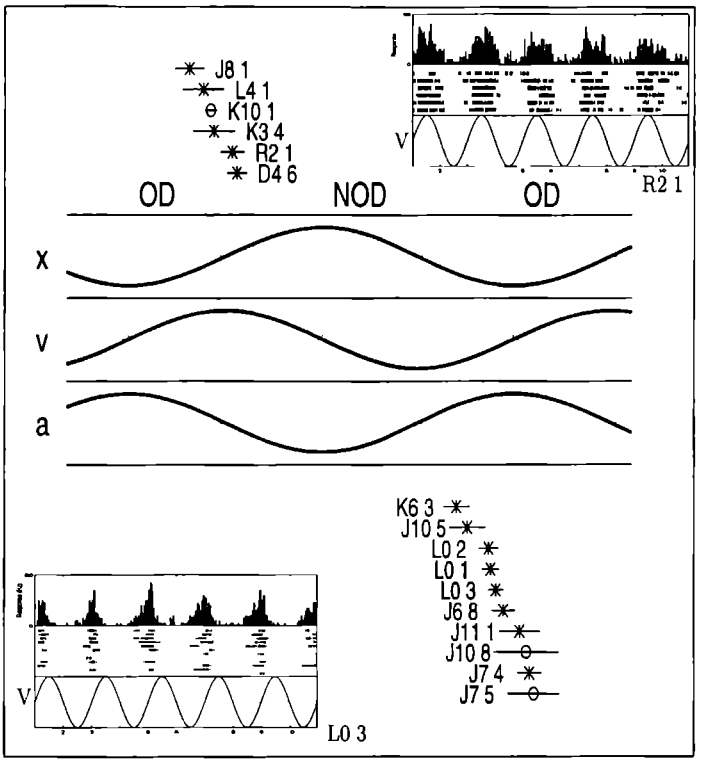


Figure 5 6 *Population plot of the mean response peak and standard deviation relative to the phase of a sinusoidal stimulation Displacement (x), speed (v) and acceleration (a) profiles are shown in optimal and non-optimal direction Note that the neurons in the upper-left corner represent the first group of neurons of which the relative phase of the response is only active in the preferred direction without any interference of rebound effects or (de-)acceleration within the stimulus An example of such a neuron (R2 1) is shown in the upper-right corner The second group is shown in the lower right corner These neurons show clear rebound effects Though these neurons are responsive to velocity, the peak response lies close to where the speed of the stimulus is zero or the acceleration is maximal in the non-optimal direction A representative example is shown in the lower-left corner (neuron L0 3)*

in Fig 5 6 (bottom) all the cells in the second group had their response peak between 307 and 379 degrees For four of these neurons the peak occurred in the OD part of the movement but a substantial part of the response (still 36 percent for neuron J7 5) occurred during stimulation in the NOD

The following features occurred frequently in the responses to constant speed stimuli

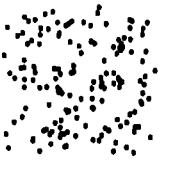
in group 2 and not in group 1 and helps explain the unexpected behavior found in those cells
i) An inhibitory period directly after the phasic response, while still stimulating in the OD (found in 7 neurons, all belonging to group 2)
ii) A post-inhibitory rebound after/during stimulating in NOD (found in 9 cells)
iii) An inhibitory response in NOD (found in 8 cells) and an inhibitory OFF-response after termination of movement in the OD (K6 3)
Six cells (J7 5, J10 5, J11 1, L0 1, L0 2, L0 3) showed the all three types of behavior (for example L0 2 Fig 5 3A,B at low speed) All these cells belong to the second group

Can the constant speed responses predict the responses to oscillation?

During oscillations the tonic responses differ from those seen in constant speed trials in that there is a possible history effect The tonic response could be boosted by the release of inhibition caused by the preceding part of the movement (postinhibitory facilitation)

To examine this possibility that the summation of the response in the OD and the rebound response in the NOD could explain the increase in motion contrast during oscillation, the motion contrast and relative phase were calculated from the constant speed trials by superimposing the responses during constant speed in the OD and NOD in such a way that onset of the OD histogram coincided with the end of the NOD histogram Thus, for example, the rebound excitation from stimulation in the NOD as seen in e g Fig 5 1B is added to the phasic response from Fig 5 1A which resulted from stimulation in the OD Motion contrast and relative phase were calculated by the same procedures as used for the oscillation data i e by fitting a gaussian to the response peak The time of the maximum of the fitted gaussians was used to obtain relative phase and the mean firing rate in the half-cycle surrounding the maximum as AFR_{opt} and during the other half-cycle as AFR_{n-opt} The results of this analysis are shown in Fig 5 7 In the left panel it can be seen that the predicted motion contrast for oscillation is considerably higher than for the superimposed constant speed data The mean difference over all cells is 0 3 and this difference is significant (paired t-test p = 0 0007) In the right panel we observe that relative phase for oscillation is considerably lower than for the superimposed constant speed data The mean difference over all cells is 40 deg and this difference is significant (paired t-test p = 0 0009) The effective frequency of the superimposed data was 0 33 Hz for a constant speed trial length of 1 5 sec and 0 45 Hz for a constant speed trial length of 1 1 sec These frequencies are always in the range of frequencies used in the oscillation trials As the relative phase during oscillation depended only weakly on frequency the relative phase from oscillation and superimposed trials can be compared directly The motion contrast during oscillation depended quite strongly on frequency but in general did not vary much in the range 0 25 to 0 5 Hz which is the range of the superimposed trials In summary, these results show that a simple superposition model cannot explain the responses of these cells during oscillation since both oscillation response contrast and relative phase differ considerably from those observed experimentally

Summation of OD and post-NOD responses is the simplest form of interaction One



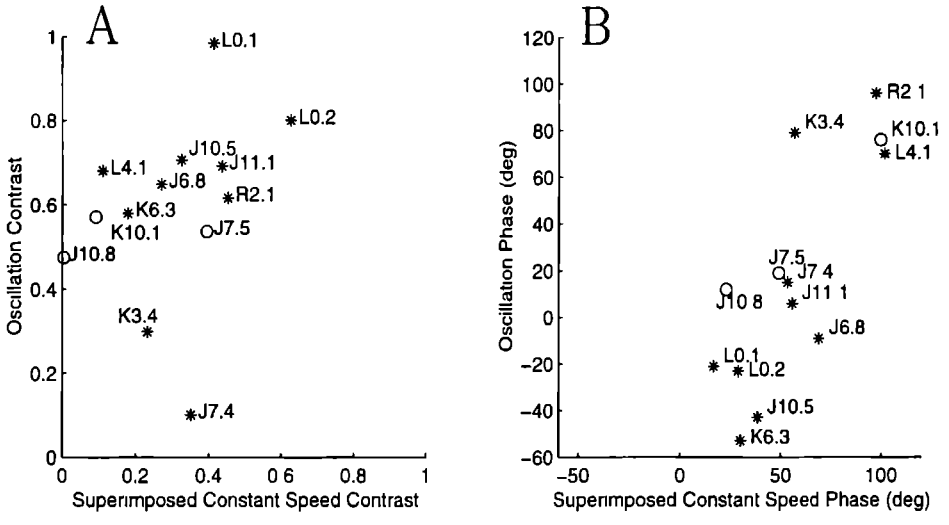


Figure 5.7: *Comparison between the superimposed constant speed responses and the responses to sinusoidal oscillation. In panel A the contrast based on the superimposed AFR in OD and NOD (see methods) is plotted against the contrast during oscillation (alternating OD and NOD). In panel B the phase relation for both conditions are shown. The star-marked neurons were tested for translation, the circle-marked for divergence.*

might argue that somehow the timing of the overlap may have been better than predicted from superposition. In that case an optimization of the interaction could perhaps lead to a better estimation of the observed motion contrast during oscillation. This idea was implemented by optimally aligning the response in the OD and NOD (see Fig. 5.8A and B). This method estimates the maximal possible contrast based on constant speed trials. As we see in Fig. 5.8C, in this case there is no significant difference between the estimated constant motion contrast (shifted and summed) and the real oscillation contrast (paired t-test, $p = 0.5$, n.s.). Since the responses are shifted by different times to obtain AFR_{opt} and AFR_{n-opt}, one cannot get a meaningful estimate of relative phase from this procedure. This result does show that motion contrast during oscillation can be obtained by an optimization of timing of the constant speed responses. However, it was clear that there was no systematic shift which had to be used to get the optimization. This result does show that motion contrast during oscillation can be obtained by an optimization of timing of the constant speed responses but the shifts required are random, making it unlikely that superposition was underlying the response enhancement during oscillations.

The oscillation seems to shorten or prolong the onset of the tonic response in the NOD based on the frequency of the stimulation. At this point, one can only speculate about the mechanism involved. The notion that sinusoidal stimulation picks up the

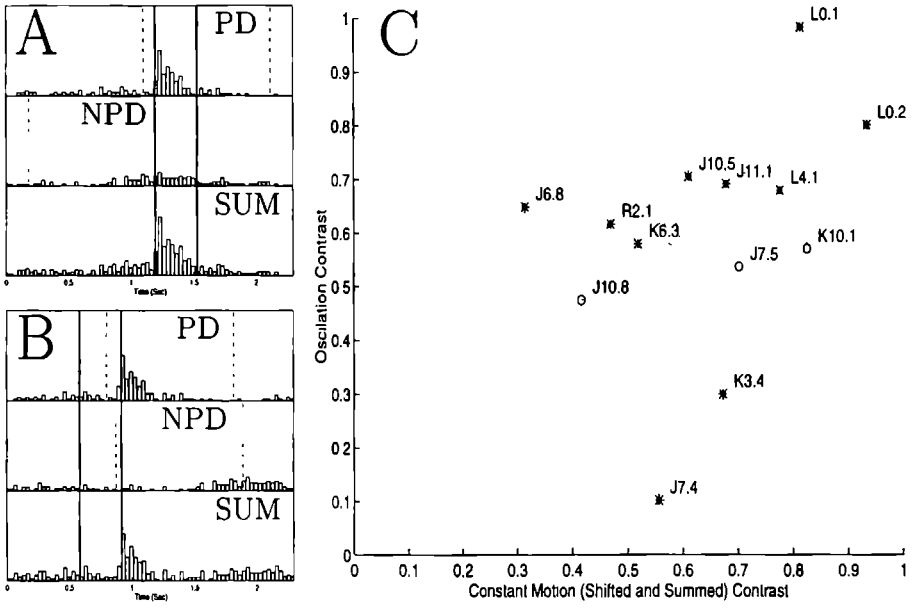


Figure 5.8: *A: The summation (AFR_{ss-opt}) of the OD and NOD for neuron J11.1, shifted relative to each other to obtain an estimation of the maximal response when both stimuli coincide. The dot-stripe marker indicates stimulus on- and offset. The solid marker indicates the area over which AFR_{ss-opt} was calculated. B: The summation ($AFR_{ss-n-opt}$) of the OD and NOD for neuron J11.1, shifted relative to each other to obtain an estimation of the minimal response when both stimuli coincide. The dot-stripe marker indicates stimulus on- and offset. The solid marker indicates the area over which AFR_{ss-opt} was calculated. Note that area with minimal response in the NPD is not during stimulation because of the lack of inhibition (Compare to Fig. 5.1B or Fig. 5.2B). C: Comparison between the oscillation contrast and constant speed contrast. Dotted lines indicate SE. To obtain an estimate of the maximal possible contrast, first the shifted and summed average response (AFR_{ss-opt}) was calculated as the sum of the maximal response during PD and NPD for a period (sliding period to get maximum) of 1/3 the stimulus duration (Panel A). Second the shifted and summed average response ($AFR_{ss-n-opt}$) was calculated as the sum of the minimal response during PD and NPD for a period (sliding period to get minimum) of 1/3 the stimulus duration (Panel B). The constant speed, shifted and summed, contrast index was then calculated based on these two measures: $(AFR_{ss-opt} - AFR_{ss-n-opt})/(AFR_{ss-opt} + AFR_{ss-n-opt})$. Note that the fraction of the total stimulus duration (here 1/3) used to calculate the contrast, reflects in the contrast measure. A smaller fraction would result in higher peak and lower valley values, and therefor in a higher contrast. The value 1/3 was chosen because it captures the complete rebound response of most neurons without including any inhibitory zones.*

frequency estimate quicker than the constant speed oscillation (Fig 5 3A,B) suggests that acceleration and deceleration of the flow speed could be a factor in getting a quicker and more precise prediction There are several problems with the explanation discussed above The first problem is that it fails to account for the phase-locking with fixed relative phase and thus a variable time delay across different frequencies Second, one should find inhibition during movement in the OD and/or NOD An example of a neuron that is selective for temporal periodicity but shows no inhibition during constant speed stimulation is K6 3

Reversal in direction selectivity

A clear example of unexpected behavior during oscillation is given in figure 5 9 During constant speed stimulation neuron K6 3 gave both a phasic and a tonic response, and did not show any inhibition figure 5 9A,B During oscillations, a prominent phasic response was only seen during the onset of the oscillatory stimulus In later cycles the main responses occurred for movement in the NOD direction and the peak occurred near the end of this period (maximum deceleration) For the constant speed stimuli, for all 8 directions tested, there was no suppressive response during the periods of stimulation In contrast, during oscillation there is a clear suppression for movement in the OD If one shows the optimal stimulus after this nonoptimal one, a strong inhibition would be seen De facto this results in a complete reversal of optimal direction

5.4 Discussion

In this chapter, neurons were presented which were specifically sensitive to temporally periodic patterns Two characteristics of these neurons lead to the conclusion that these cells in VIP form a class of "periodic-pattern neurons" First, the responses of the neurons were phase-locked to stimulus velocity with a relative phase that was independent of the driving frequency Surprisingly, for many cells the response peak during oscillation occurred during motion in the NOD Second, most of the neurons showed a larger motion contrast (modulation of response) during oscillation trials than during constant speed trials The enhanced motion contrast during oscillation was caused both by an enhanced response during motion in the OD and an enhanced suppression during motion in the NOD

The finding of enhanced facilitatory responses during oscillations could not be predicted from a simple superposition model where the responses to constant motion in the OD and NOD are added This mechanism is basically the same as the superposition mechanism first introduced by Hubel and Wiesel (1959,1962) The latter authors speculated that the direction selectivity of some simple neurons in V1 of the cat might be due to the superposition of, on the one hand, the facilitation due to a light bar entering an ON region and, on the other hand, the rebound facilitation due to the release from inhibition caused by the same light bar leaving an OFF subregion This idea of Hubel and Wiesel was later supported by some models of direction selectivity (Duysens et al ,

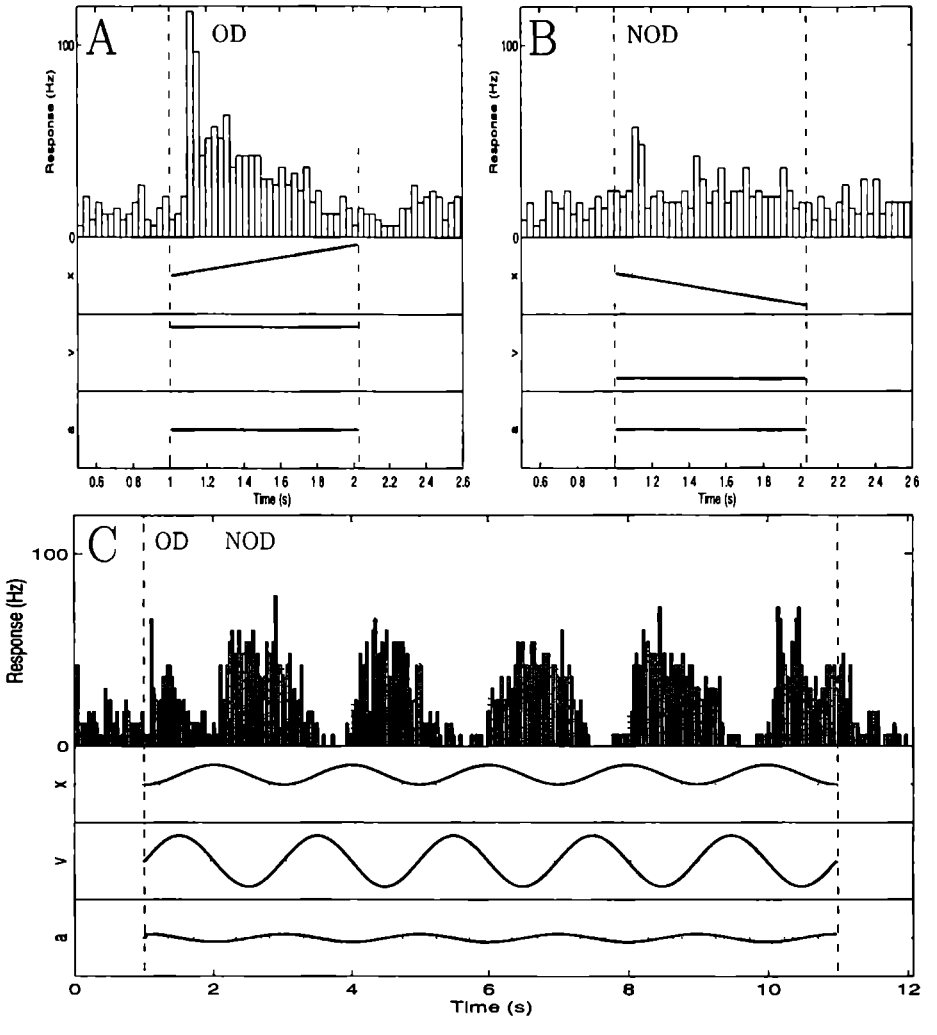
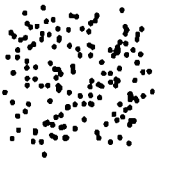


Figure 5 9 *A,B Responses of the neuron K6 3 to translation in the OD and NOD (Speed was 33 3°/s) C Responses of the neuron K6 3 to an sinusoidal modulation of the translation speed (max speed 33 3°/s) The responses are shown as the averaged histogram (33 2 ms bin) The speed modulation of the translation stimulus is shown at the bottom of each panel*

1987) In the present study, the response enhancement in the optimal direction of some cells might be understood in terms of the summation of a facilatory response in the OD



and rebound or late facilitation in de NOD (see for example neuron L0 2 of Fig 5 3) However, the mechanism cannot explain the data of the whole population A superposition of the responses to constant speed stimulation in the OD and the NOD leads to a motion contrast and relative phase that are different from the one observed during oscillation if the population as a whole is considered (Fig 5 7)

A second element contributing to the crispness of the responses to oscillations is related to the enhanced suppression during the "non-optimal" half of the cycle This finding of enhanced suppression during oscillations is equally difficult to explain on the basis of the responses to single constant speed presentations (compare for example part A and E of Fig 5 1 based on neuron J10 5) A possible explanation is that the suppressive responses may be completely masked by the phasic onset responses which are only present during the constant speed presentations or during the first cycle(s) of the oscillations However, this is not very likely since the period of suppression during oscillations are usually broader than the phasic onset responses mentioned

Active versus passive vision

Since passive visual mechanisms fail to explain the observed responses during oscillations it is worthwhile to consider other mechanisms, such as those related to "active vision" Consider for example the evidence for anticipatory activity in the intraparietal cortex The lateral intraparietal region (LIP) adjacent to VIP was shown to contain neurons which are more active before the appearance of a predictable saccade target than before the predictable appearance of the same target when it is irrelevant to the animal's behavior (Colby et al , 1993a) They concluded that about 40 % of the neurons in LIP anticipate the retinal consequence of an intended saccade Could anticipation play a role in the present VIP data as well? The oscillating stimuli were highly predictable The response increase at the end of the movement in the NOD can be seen as anticipation of a OD movement for which the cell is tuned (if one determines the tuning based on MFR) or the anticipation of an object slowing down to zero velocity

Anticipation may also play a role in the observed build-up of the facilitatory responses over the first few cycles (see for example neuron J10 5 in Fig 5 1) This phenomenon was observed in 6 of the 16 neurons described here This building up of the responses over several cycles was limited to the tonic response parts An alternative explanation is based on the known effects of attention on responses of various parietal cells (Bushnell et al , 1981) It is indeed conceivable that the build-up is a manifestation of the increment in effort and attention made by the monkeys as they tried to suppress eye movement in relation to the moving background, which represent a strong optokinetic stimulus Furthermore, the present data indicate that acceleration and deceleration may also be important in this respect The notion that sinusoidal stimulation picks up the frequency estimate quicker than the constant speed oscillation (Fig 5 3A,B) suggests that acceleration and deceleration of the flow speed could be a factor in getting a quicker and more precise prediction

Are the presently described results specific for VIP? There have been no studies yet with oscillatory stimuli in MSTd However, recently Duffy and Wurtz (1997b) showed

that for 85 % of the neurons they studied in MST a preceding stimulus had an effect on the early response of an immediately following stimulus The impact of this effect was proportional to the response to the preceding stimulus They concluded that the responses are influenced not only by the stimulus present at any given moment, but by other recently presented stimuli as well

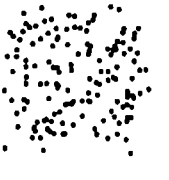
Phasic and tonic responses

In the constant speed presentations, the phasic responses of VIP neurons dominate and they underlie the direction selectivity However, during oscillations the main response is the tonic one, and in some cases this response falls in the NOD part of the cycle, thereby creating an apparent reversal in direction selectivity A difference in direction selectivity of phasic and tonic responses is not a unique feature of VIP Based on data obtained using stimuli which are similar to the present ones, Duffy and Wurtz (1991) concluded that in MST "the phasic response was nearly always less selective for stimulus motion than the tonic response" Along the same lines, Colby et al (1993b) showed an example of a VIP neuron in which the tonic response part showed a larger orientation selectivity than the phasic part (their Fig 10) The present data show that phasic responses to onset of stimulation often are misleading with respect to direction selectivity, and that it is very useful to add oscillatory stimuli to get insight in the direction selectivity and phase-locking of visual cells

Functional significance

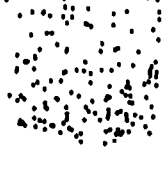
One can speculate if any neural correlate of the capability to recognize biological motion could be found in monkey cortex The cells discussed in this chapter are likely candidates the finding that their responses are phase-locked to the stimulus makes them good candidates to signal the presence and frequency of periodic motion In order to serve as a neural substrate for coding periodic motion the cells need to cover the possible relative phases uniformly This condition is analogous to the condition that all possible orientations need to be represented in V1 in order to say that orientation of bars is represented in V1 From Fig 5 6 is seems as the cells do not uniformly cover all possible relative phases, but only covering about half of the possible ones However, the relative phases in this figure refer to the optimal direction irrespective of what the direction was in space (e g cell J10 5 has its OD in the direction of -45 degrees and cell L0 2 in the direction of 135 degrees) Effectively, the procedure of referring relative phase to the OD transforms the sample from vector data (range 360 degrees) to axial data (range 180 degrees) A standard procedure in circular statistics (Fisher, 1993) to undo this transform is to double each angle The test by Rayleigh (Fisher 1993, p70) to test the sample of relative phases (with angles doubled) for uniformity showed the deviations from non-uniformity to be nonsignificant ($p = 0\ 68$) Thus, the sample of cells observed cover the possible relative phases uniformly Note however that there seems to be evidence for clustering around the maximum speed (group I) and zero-crossing (group II)

In the present study full-field optic flow patterns were used In a natural environment,



these patterns could only result from self-motion It is an open question if these neurons might be useful in detecting biological motion in the visual surround, as the motion of other animals in the surround are unlikely to be larger than a few degrees of visual angle It is tempting to relate the high VIP sensitivity for oscillations to egomotion (such as caused by locomotion or body sway) VIP cells receive input from vestibular sources (Graf et al , 1995) and it would therefore be of great interest to know whether such vestibular responses exhibit the same direction selectivity as the visual responses (in fact such convergence may be crucial in the avoidance of motion sickness) It would also be informative to compare the temporal aspects of the responses to vestibular and visual inputs The vestibular system is dominantly coding for acceleration and deceleration and there should be VIP responses to these components The present findings suggests some sensitivity to visual acceleration and/or deceleration component of the visual stimulus Such sensitivity would be in line with vestibular responsiveness

In conclusion, in VIP a special effectiveness of oscillatory stimuli was demonstrated In fact, as mentioned in results, there are neurons which gave only perceivable responses to oscillations and not to constant speed stimuli Hence the present data complement the results of von der Heyd et al (1992) for gratings These authors found that some neurons in the monkey visual cortex fail to respond to bars and edges while they were vigorously activated by moving gratings The data presented in this chapter show that such results do not necessarily rely on spatial periodicity Temporal periodic stimulation is by itself very potent in activating visual cortical neurons, in casu those in VIP

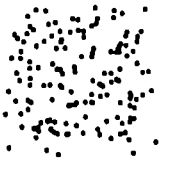


Chapter 6

Smooth pursuit coding in VIP

6.1 Introduction

The detection of how we move with respect to the environment (egomotion) and how objects move towards us is of primary biological importance Several sensory signals can help in this task The vestibular systems signals head movement, the somatosensory system detects when we touch approaching objects and most importantly, optic flow on the retina provides heading direction information How are these signals combined? Retinal optic flow signals have to be combined with extraretinal signals to allow the detection of heading during smooth pursuit (Pekel et al , 1996) There is now good evidence that this occurs in the medial superior temporal area (MST, Bradley et al ,1996) Hence we start to understand how the step is made from a retinal coordinate system to an external ("screen") coordination system (Bradley et al ,1996) But the question remains how this information is further processed Signals from MST are send to VIP (Boussaoud et al , 1990, Baizer et al , 1991) In the latter area there are neurons which respond to smooth pursuit (Colby et al , 1993b) Furthermore it was shown in previous chapters, that many VIP neurons can be activated by optic flow stimuli related to egomotion (divergence, convergence, rotation, fanning etc , Schaafsma and Duysens, 1996, Schaafsma et al ,1997) Since many VIP neurons are sensitive to somatosensory (Duhamel et al , 1991) and vestibular input (Graf et al , 1996) it is tempting to speculate that this area provides a further step in the integration of egomotion related activity (translation from space coordinates to body coordinates, VIP neurons respond to somatosensory stimuli, see Colby et al , 1993b) So far the data on VIP is very limited Colby et al (1993b) described 17 VIP cells which were active during smooth pursuit They found that some of these cells could be activated by stimuli translating in the same or in the opposite direction of the optimal smooth pursuit direction but further details about the exact tuning are not available Nor is it known whether these pursuit cells are responsive to optic flow stimuli (similar to MST, Bradley et al , 1996) Furthermore, the tests for smooth pursuit were carried out with unidirectional ramp and hold stimuli, which make it often difficult to exclude that eye position was coded rather than eye movement



6.2 Results

To answer some of these remaining questions the present study compares the smooth pursuit responses to visual responses, not only to translation but also to first order optic flow (for details of the methods see chapter 2) Furthermore a circular moving dot was used as the smooth pursuit inducing stimulus (Thier and Erickson, 1992) The advantages of this type of stimulus is that all possible directions are tested while usually only a few directions are tested with ramp and hold stimuli Furthermore, by testing the cells both with a clockwise and counterclockwise moving dot one can determine whether the responses depend on eye position or on eye movement This is illustrated in Fig 6 1

The first neuron, shown in the upper two panels (A for clockwise and B for counterclockwise pursuit) of figure 6 1, responded to the position of the eye As indicated by the small arrows, response was always maximal when the direction of gaze was towards the far left position on the screen The second cell, shown in the two lower panels (C and D for cw and ccw pursuit respectively), was a typical smooth pursuit neuron The optimal direction for smooth pursuit was the same for clockwise and counterclockwise movement of the fixation dot Furthermore, responses to these two directions of rotation occurred when the direction of gaze was at different positions Therefore eye position can be excluded as being the primary source of the responses In total 118 cells were investigated for oculomotor responses Six of these belonged to LIP while all the others were from VIP The LIP cells responded in relation to saccades while in VIP such responses were absent Of the 112 VIP cells tested with stimuli as shown in Fig 6 1, a total of 33 cells was active during smooth pursuit of a circular dot moving against a dark background Within this sample, 8 cells were tested both with clockwise and counterclockwise movement (cw and ccw respectively) Three of these cells were mostly location sensitive (as the one shown in Fig 1A and B) while three cells were purely pursuit cells (see for example the neuron in Fig 6 1C and D) Two responded to both location and direction of smooth pursuit Response was therefore not on the same location, nor optimal for the same direction while following a dot clock or counter clockwise

For the 28 cells showing no location sensitive tuning, an optimal direction of smooth pursuit was calculated using the method described by Thier and Erickson (1992) This is shown in Fig 6 2 As far as can be judged from the limited number of cells, there was no systematic bias for any particular direction (Fig 6 2) From the ten neurons tested for optic flow, nine were tested for translation in eight directions

When this optimal direction was compared to the optimum translation direction (determined during steady fixation trials) it was found that there were surprisingly few cells for which the direction was close to being either opposite (180 deg difference) or the same (0 deg difference) with respect to the optimum smooth pursuit direction A typical cell is illustrated in Fig 6 3 (same cells as indicated by arrow in Fig 6 2B)

When tested with the circular moving dot, this cell responded optimally to movement to the bottom right (319 $\pm$ 23 deg) However, when the monkey fixated (to a point at the center of the circular path, see Fig 6 3) the translating stimuli which were most effective (amongst the 8 directions tested) were from left to right (ϕ_0 = 11 $\pm$ 10 deg, across the receptive field indicated by the inner square in Fig 6 3) For MST it has been

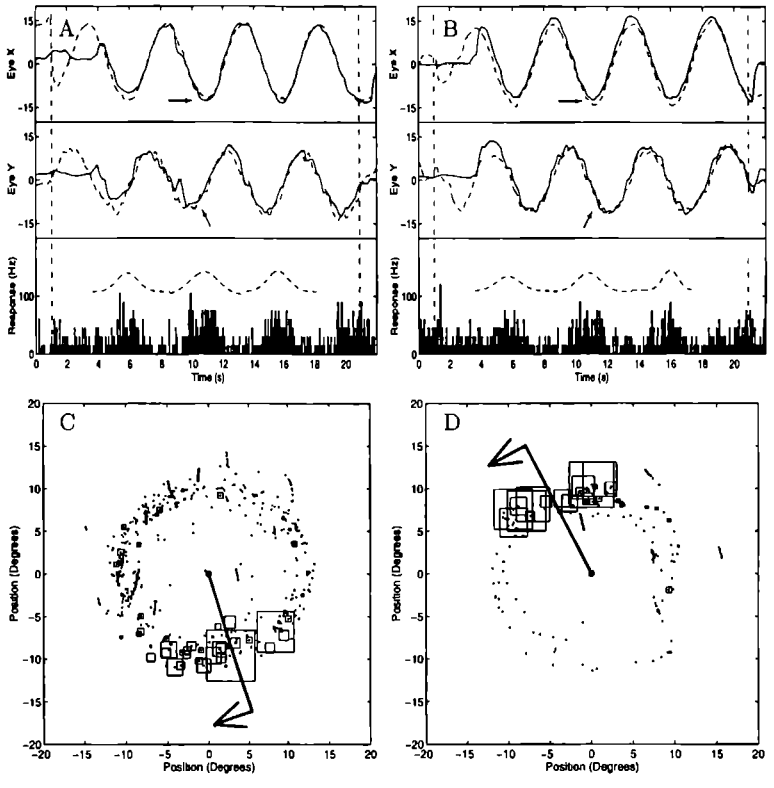


Figure 6.1: *Responses of two VIP cells to smooth pursuit (cw and ccw). A,B: For two trials the eye movements in the horizontal (X) and vertical (Y) are shown in the two upper panels. The responses are shown in the averaged histogram (33.2 ms bin). The cumulated trials are fitted with a Gaussian. The result of these fits is shown by the dotted line above the histogram (shifted upward for clarity). The arrows indicate the gaze direction (in x and y direction) eliciting the maximum response. C,D: Both panels show a section of the visible screen with position (x,y)=(0,0) deg as the center and the fixation point. For smooth pursuit trials, the eye jumped to position (12.5,0) deg. and then moved clockwise (C) or counterclockwise (D) to follow a dot of 0.64 deg diameter. Cell firing during smooth pursuit is represented as squares, the diameter of which is proportional to the firing rate in 75 ms bins (the maximum response was 316 Hz and 331 Hz for one bin in panel C and D respectively). The thick line through the middle of the smooth pursuit circle indicates the position at which the maximum response during smooth pursuit was encountered (estimated by fitted Gaussian over the cumulated trials as shown in panels A and B for a different cell). The thick arrow is the optimum direction of eye movement. Note that panel A and C represent clockwise smooth pursuit and panel B and D ccw.*

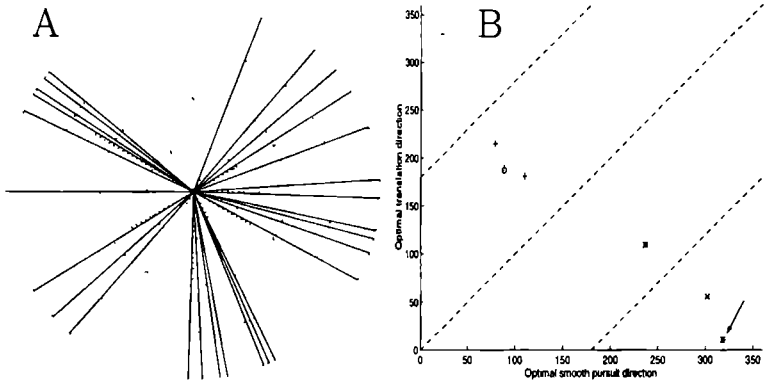


Figure 6.2: *A: Optimal direction of smooth pursuit for VIP neurons. B: Comparison of the optimal direction of smooth pursuit and the optimal translation direction. The different markers indicate the preference of that neuron for first-order optic flow: * = expansion, o = rotation, + = spiral optic flow (combination rotation and divergence), x = no tuning, . = not tested. The dashed lines represent the standard deviation. The optimal smooth pursuit direction it is obtained from the fit by a gaussian as shown in fig. 6.1A,B. The optimal translation direction was obtained from fitting a Batschelet distribution through the data points (see Schaafsma and Duysens, 1996). The arrow identifies the neuron shown in fig. 6.3.*

reported that the preferred direction for translation for pursuit cells depends on the size of the stimulus (Komatsu and Wurtz, 1988b) To investigate whether such size factor could explain the difference between oculomotor and visual optimum direction, the VIP cell from Fig. 6.3 was tested with translation stimuli in eight directions presented over each one of nine subsections of the field. The responses were significant for 7 of the 9 sections (Fig. 6.3 bottom; length of arrow indicates strength of response). The direction selectivity was maintained for almost all subsections (response in the preferred direction towards the contralateral side being between 30 and 110 percent larger than the best response for ipsilaterally directed movement). There was only one exception namely the subsection which included the fixation point. For this field the neuron was bi-directional tuned. The second best response was perpendicular to the direction of the translation of the best response.

To study the interaction between the smooth pursuit and the translation, both were combined in an additional experiment. During smooth pursuit the addition of translating stimuli moving in the preferred direction enhanced the AFR (averaged firing rate over one full cycle) during the complete stimulation cycle by 230 percent (not shown). In the non-preferred direction of translation this enhancement was still considerably large, namely 74 percent. When compared to the responses to the translation stimuli only, the combined responses were the same order and was only slightly facilitated by the eye

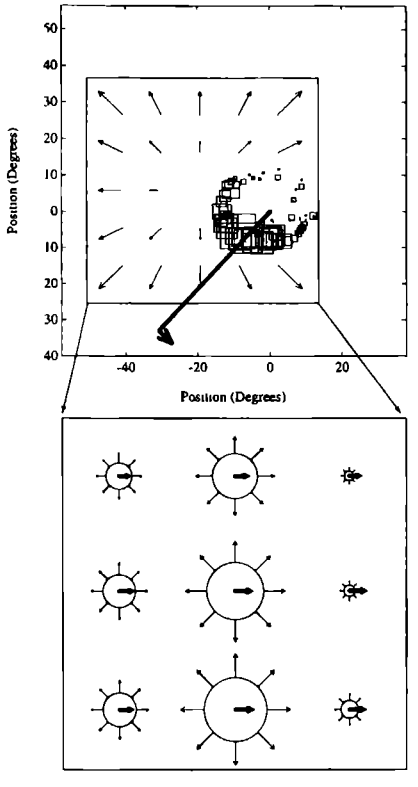


Figure 6.3: *Responses of an VIP neuron during circular smooth pursuit (top) and to translation and divergence stimuli presented over one of nine subsections of the receptive field (bottom). The top shows a section of the visible screen with position (x,y)=(0,0) deg as the center and the fixation point for testing the receptive field (square with divergent pattern; max. response: 47 spikes/s). For smooth pursuit trials, the eye jumped to position (12.5,0) deg. and then moved counterclockwise to follow a dot of 0.64 deg diameter at a speed of 16 deg/sec. Cell firing during smooth pursuit is represented as squares, the diameter of which is proportional to the firing rate in 150 ms bins (max. response: 45 spikes/s). The thick line through the middle of the smooth pursuit circle indicates the position at which the maximum response during smooth pursuit was encountered (estimated by fitted Gaussian over the separate trials resulting in a mean maximum response of 45 +/- 5 Hertz). The thick arrow is the optimum direction of eye movement. At the bottom the averaged responses to the optimal translation direction (arrows) and divergence (circles) are shown (radius or length of arrows correspond to mean firing rate; maximum response for translation and divergence: 23 and 37 spikes/s, respectively). The stimuli were shown in a 3x3 grid of size 21 x 21 deg each. The divergent patterns were scaled proportionally to the stimulated area. Note that the size of the receptive field (top figure) was estimated based on responses to translation.*

movement response

The neuron shown in Fig 6 3 was 1 out of 7 cells tested with first order optic flow stimuli (divergence, convergence, CW and CCW rotation or combinations of them) It responded only to divergence over the RF (inner quadrangle in Fig 3) and to mixtures of divergence and rotation (not shown) One of the characteristics of MST cells is that they maintain their selectivity when the same type of stimuli is presented over smaller subsections of the receptive field In this respect it is of interest that the presentation of scaled-down expanding stimuli over small subsections (one ninth of the RF) yielded significant responses in 6 of the 9 sections (largest responses for the 3 middle positions, see Fig 6 3 bottom) Six other neurons were tested for first-order optic flow Of these, 2 responded best to rotation, 1 more to divergence and 2 to spiral stimuli respectively On neuron did not show a significant tuning

6.3 Discussion

In conclusion, the present data confirm the findings of Colby et al (1993b) that a large proportion of VIP cells respond during smooth pursuit (59 % in their study, 29 % in the present) The quantitative comparison of optimum pursuit and translation stimuli do not support the notion that these two types of directions are either the "same or opposite", as expected on the basis of previous reports, either in VIP (Colby et al , 1993b) or in MSTl (Thier and Erickson, 1992) This difference may be related to differences in definitions (how large can a deviation be to fall outside these two classes of "same" and "opposite"?) and methods (size of the dots, hand plotting in the MSTl study etc) At any rate, the presently observed difference in oculomotor and visual direction preference argues against the notion that the responses during smooth pursuit may have been caused by passive visual properties and supports the proposition of Colby et al (1993b) that in some VIP cells an extra-retinal input plays a role in the responses during pursuit

In addition the data show that such smooth pursuit cells can respond to first order optic flow stimuli, as might have been expected on the basis of the recent work on MST (Bradley et al ,1996), an area which projects to VIP This makes VIP an attractive candidate for the analysis of body heading direction during smooth pursuit eye movements

The more accurate perception of the direction of heading during real as compared to simulated pursuit eye movements made Royden et al , (1992) to conclude that extraretinal oculomotor signals are essential for the former task under most but not all (Van den Berg 1992,1993) conditions Essential for this notion is the question whether indeed the brain contains neurons which respond both to smooth pursuit and to optic flow stimuli such as used to detect heading direction (Banks et al , 1996) In this study we showed that neurons in VIP do respond optimally to diverging optic flow stimuli and smooth pursuit For example the large sensitivity of the middle part of the receptive field of the cell shown in fig 6 3, could underlie the ability to discriminate heading direction during forward locomotion The additional responsiveness to smooth pursuit of targets moving away from the focus of expansion makes cells of the type described here, well-suited to maintain a role in heading perception even when subjects are moving forward while

fixating objects along the road.

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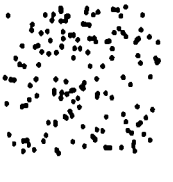


Summary and Conclusions

This thesis presents a set of experiments aimed at understanding a cortical area that has been neglected if one compares it to other areas It was known that this area responded to more than one modality, but unlike an area as for example the superior colliculus which is multi-sensory and heavily involved in saccades (quick eyemovements) it has never drawn much attention

Lately, there is an increased interest in integration of the different modalities of sensory information The results presented in this thesis suggest that there is a lot of integration in VIP between the visual system, the somatosensory system, the vestibular system and eyemovement related areas All data points in the direction that VIP is involved in generating a percept of the orientation of the body in a 3D environment

The first objective was to compare VIP to MST for responses to optic flow Most VIP neurons showed clear direction selective responses for either translation, expansion, contraction, clockwise or anti clockwise rotation VIP was in particular sensitive to expansion but sometimes also to a combination of components (spiral stimuli) A typical feature of VIP neurons is that their responses to these optic flow components remain when different parts of the receptive field (RF) are stimulated separately ("scale invariance") For the most responsive sub-field the response was on average 93 percent of the whole field response For all sub-fields the mean response was on average 64 percent of the whole field response To test whether the scale invariance arose from convergence of translation sensitive sub-fields with radial or circular direction preferences ("mosaic hypothesis"), the direction selectivity for translating stimuli was tested over these sub-fields Basically the direction selectivity for translation was unchanged in the various sub-fields, thereby excluding the direction mosaic hypothesis

Since there are some reports of MST neurons being responsive to rotations of a plane, VIP neurons were tested for fanning Fanning is the mathematical equivalent of a fronto-parallel plane rotating around a fronto-parallel axis Fanning did effectively induce responses in VIP neurons Most often the responses were almost as strong as for translation, expansion/contraction or rotation, indicating that there was no special sensitivity for rotation in depth For neurons, sensitive to expansion, the response to fanning could often be explained by the positioning of the expanding part of the fanning stimulus over the area which was most responsive to expansion For neurons which were direction selective to translation, the optimal direction of fanning was usually the same as the preferred direction for translation It is concluded that VIP neurons may be sensitive

to movement of structured planes but they are not specialized for the detection of such movement

By presenting stimuli for various durations, the minimum duration needed to elicit direction selective responses was determined Random dot expansion patterns presented for only 2 frames were found to be already effective to elicit responses On average such responses augmented by increasing the duration of the stimulus presentations up to 46 ms for translating stimuli and up to 118 ms for expanding patterns At longer stimulus durations the tonic part of the response became increasingly important (occasionally even showing stronger direction selectivity than the phasic part of the response) It is concluded that cells in VIP are well-placed to underlie the ability to detect optic flow patterns of short duration

All neurons investigated responded to the oscillatory stimuli, provided the optimal optic flow component was present In some cases there was a clear build-up of responses over the first few cycles Some neurons gave only a very small response to single motion stimuli, but responded vigorously to an oscillating optic flow pattern Efficacy of oscillating stimuli could be accounted for by an enhancement of the direction selectivity, due to facilitation of tonic facilitatory components in one direction and increased suppression in the other In some cases the larger responses during oscillation were due to summation of disinhibition, following stimulation in the non-optimal stimulus direction (NOD), and facilitation due to movement in the optimal direction (OD) Furthermore, in single presentations a phasic onset response often dominated the direction selectivity while this was not the case after a few cycles of oscillations This explains why some neurons showed a reversal of the preferred direction when single motions were replaced by oscillating ones

Evidence was presented that there is indeed a convergence of optic flow and smooth pursuit information in VIP, suggesting that there is an overlap between the smooth pursuit class of cells and the population of optic flow coding cells As found by others for the lateral part of the medial superior temporal area (MSTl), some pursuit cells responded to translating patterns when the eyes were held stationary However, some of these units also showed a high sensitivity for optic flow components such as divergence

The similarities between VIP and MSTd are much more striking than the differences with regard to optic flow responses and smooth pursuit although neurons in MSTd do not respond to somatosensory sensations MST, like VIP, does receive vestibular input Therefore there is reason to expect area MSTd to contain cells responding to oscillatory stimuli in a way that was found in VIP if this behavior is related to vestibular stimulation

Discussion and directions for further research

The data presented in this thesis are better accommodated by what Duffy and Wurtz (1991b) termed the vector field hypothesis, which is basically the same as the compartment model proposed by Saito et al (1986) In this model, proposed to explain the RF structure of MSTd neurons, the local detection of rotation or divergence is achieved by projections of the appropriate MT afferents onto single branches of MSTd neurons The input to one such dendrite may be enough to generate a response of one particular neuron and this can lead to, for example, local divergence detection Sensitivity profiles for local presentations of optic flow are also well explained by this model since one simply has to assume that the contribution of one of the dendritic branches is more dominant The advantage of this model is that no neurons have to be postulated which can act as pure local divergence detectors since the dendritic trees incorporate this function

An explanation and implementation of such a scheme has been presented by Zhang et al (1992) It provides a mechanism for position invariance based on the combination of an inhibitory response for the (local) non-preferred direction and an excitatory response which increases linearly with speed This model predicts the same local responsiveness to translation as the direction mosaic hypothesis Local inhibitory responses were infrequently seen in the present study In this thesis, evidence will be presented that VIP neurons maintain their response when an optimal stimulus, such as divergence, is scaled down and presented over a smaller section of the RF It would be interesting to see whether the selectivity for a particular optic flow pattern is the same throughout the receptive field ("directional position invariance") Some of the data suggests that that is the case (Chapter 2, compare Fig 2 10B and Fig 2 11B)

During the study presented in this thesis, the stimuli were limited to a few basic optic flow components translation, fanning, rotation, divergence and combinations of these This is the common procedure to study optic flow responsive cells in the visual cortex By presenting the same stimuli scaled over a smaller subsection of the receptive field it was found that VIP cells kept responding to these stimuli (as do cells in MST) There is a lot of speculation about how this "position invariance" is achieved and what the exact underlying structure of the receptive field is The problem of distinguishing between the several proposed models is that they all predict the receptive field structure

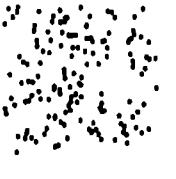
from a very limited set of optic flow stimuli Calculation of the optimum stimulus are generally done off-line and mostly by fitting/drawing tuning curves in polar plots and calculation its direction index A better approach would be to search on-line for the most optimal optic flow stimulus for any given cell Such a method does not limit the search to the basic zeroth and first order optic flow components Every possible flow field can be used to study the neurons, including higher order fields, fields with discontinuities in the flow, or transparent stimuli To be able to construct such a set of optic flow fields (e g not ordered based on Taylor expansion and rotation invariance) a neural network can be used A pilot study (not further discussed in this thesis) shows that by training a neural network with a set of optic flow stimuli and with the real neural responses from VIP cells, one can make a prediction of the optimum optic flow field for that neuron By using the predicted optimal flow field on-line to test the neuron one can adjust the connections in the neural network to better mimic the responses of the cell under study Repeating this procedure in an iterative process, this method will lead to a less biased search for the maximum response of optic flow sensitive neurons Furthermore, the same network can be used to study the underlying RF structure The characteristics of the hidden units can give clues about the wiring of the sub-units which form the receptive field If successful, the method can be adapted to optimize other types of visual (and non-visual) stimuli as well This automated receptive field search could lead to a major breakthrough in visual neurophysiology since the optimal definition of the receptive field structure of visual cells is one of the corner stones of this area of research

Samenvatting

Beweging en tijd zijn belangrijke aspecten van de visuele werkelijkheid We beleven de ene gebeurtenis na de andere, herinneren ons waar we zijn geweest, wat we hebben gedaan, en we maken plannen waar we naar toe gaan en wat we zullen gaan doen De hersenen verwerken beweging en tijd op vele manieren en op verschillende niveaus Het hoogste en waarschijnlijk tevens het meest complexe niveau is het cognitieve gedeelte Het interpreteert een continue stroom van informatie en reageert hierop op basis van gebeurtenissen uit het verleden Verder maakt het cognitieve gedeelte plannen voor de toekomst, probeert die te voorspellen en probeert de optimale strategie uit te zetten voor komende gebeurtenissen die deels voorspelbaar en deels onvoorspelbaar zijn In dit proefschrift presenteer ik een onderzoek aan een klein gedeelte van de hersenen, genaamd VIP (Ventraal Intra-Pariëtaal gebied), dat betrokken is bij het verwerken van beweging in de tijd (richting, snelheid en waarschijnlijk ook versnelling en / of vertraging) Het is mogelijk dat de complexiteit van de informatieverwerking in VIP op het niveau staat van een directe reactie op een inkomende gebeurtenis (beweging) Dit klinkt aannemelijk omdat de richting en snelheid van een beweging gemeten kunnen worden zonder tussenkomst van 'hogere cognitieve' systemen Ik zal echter laten zien dat er enkele argumenten zijn die dit bewegingsdetecterende gebied een klein stapje hoger op de complexiteitsladder van het centrale zenuwstelsel zetten neuronen in VIP gedragen zich verschillend op dezelfde bewegingsstimuli, afhankelijk van het (zeer) nabije verleden

VIP is gelegen in de visuele cortex, dat bij de mens en de aap een relatief groot deel (1/3) van de hersenen vertegenwoordigt De complexiteit van de visuele invoer is groot Wij bewegen ons door de buitenwereld terwijl ook andere objecten zich onafhankelijk van ons bewegen De beelden die op ons netvlies worden geprojecteerd, veranderen dan ook voortdurend en lang niet altijd voorspelbaar In de evolutie hebben zich een aantal neurale systemen ontwikkeld, die ertoe hebben bijgedragen dat we die beelden enigszins kunnen stabiliseren door het maken van compenserende oog-, hoofd- en lichaamsbewegingen Desalniettemin blijft de buitenwereld een complex bewegend patroon genereren op ons netvlies

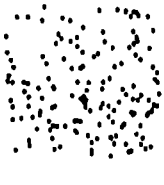
Wanneer we een bewegend object signaleren, is het niet noodzakelijk precies te weten wat het is, om in te kunnen schatten waarheen het zich ten opzichte van ons beweegt Psychofysisch en elektrofysiologisch onderzoek heeft reeds uitgewezen dat het herkennen van een voorwerp in de hersenen gescheiden gebeurt van de observatie waarheen het beweegt Hoofd- en oogbewegingen veroorzaken een goed gedefinieerd veranderend patroon (wat



we verder optische stroming zullen noemen) op ons netvlies Als de buitenwereld stabiel is terwijl wijzelf bewegen, dan is deze optische stroming goed gedefinieerd en afhankelijk van de structuur in die buitenwereld en de beweging die wij maken Wiskundig kun je laten zien dat uit de optische stroming in de meeste gevallen de exacte beweging kan worden afgeleid (op de schaal en enkele ambiguiteiten na, zoals we direct zullen zien) Psychofysische experimenten hebben laten zien dat, hoewel we onszelf goed kunnen stabiliseren op basis van optische stroming, er een complexe relatie bestaat tussen de richting waarin we kijken en een niet geheel stabiele buitenwereld (gesimuleerd)

We kunnen niet alleen onze eigen beweging en die van andere voorwerpen afleiden uit de optische stroming op ons netvlies, maar we kunnen ook de vorm van een voorwerp schatten Een (gespikkelde) roterende bol bijvoorbeeld genereert een heel andere beeld op het netvlies dan een roterende kubus De beide taken, het schatten van vorm uit bewegingen en het detecteren van zelfbeweging, kunnen niet worden verricht door alleen eenvoudigweg de bewegende patronen op het netvlies te analyseren Het is bijvoorbeeld onmogelijk om enkel op basis van optische stroming een onderscheid te maken tussen een langzaam, relatief klein voorwerp vlakbij, en een groot, relatief snelbewegend voorwerp ver weg, tenminste met één oog Ook zijn er talloze vormen te bedenken waarbij de gegenereerde optische stroming niet uniek gerelateerd is aan de exacte vorm Onder natuurlijke omstandigheden is dat nauwelijks een nadeel Immers, voor het zien van voorwerpen relatief dichtbij hebben we twee ogen, zodat het verschil tussen de beelden in beide ogen extra informatie geeft over de afstand van het voorwerp en de driedimensionale structuur Verder geven de structuur van het voorwerp, de textuur, de schaduwen en de kleur(en) extra informatie over het voorwerp, de directe omgeving en de lichtcondities Ons geheugen helpt ons ambiguiteiten op te lossen Een mooi voorbeeld is de rotatie van een egaal verlicht hol masker, dat, als het om een verticale as geroteerd wordt, altijd naar ons lijkt te kijken, zelfs als de neus van ons af staat Ook niet-visuele informatie is een goede hulp bij het verbeteren van de precisie Het vestibulaire systeem genereert informatie over hoofdbewegingen Proprioceptieve informatie (informatie over het uitrekken van de spieren bijvoorbeeld) zegt iets over lichaamsoriëntatie en kijkrichting Verder geeft het somatosensorische systeem ons informatie over beweging (bijvoorbeeld luchtstroming langs de huid) Het auditieve systeem verschaft informatie over onze relatieve positie (verandering) ten opzichte van een geluidsbron De reflecties van geluid geven tevens een idee van de grootte en structuur van onze directe omgeving In dit proefschrift komen enkele van deze modaliteiten aan bod, maar het belangrijkste onderwerp is optische stroming wat zijn de eigenschappen van neuronen in VIP met betrekking tot het analyseren van optische stroming?

In dit proefschrift wordt een studie gepresenteerd naar VIP, een hersengebied dat relatief weinig is onderzocht Het was bekend dat neuronen in dit gebied reageren op stimuli voor verschillende zintuigen Maar in tegenstelling tot bijvoorbeeld een gebied als de superior colliculus, waar multi-sensoriele informatie wordt verwerkt en dat is betrokken bij snelle oogbewegingen, is VIP veel minder bestudeerd De laatste jaren is er een toenemende belangstelling voor de integratie van de verschillende modaliteiten van sensoriele informatie De resultaten die gepresenteerd worden in dit proefschrift laten zien dat er een convergentie plaatsvindt van visuele informatie en oogbewegingsinformatie in VIP

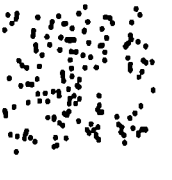


Andere onderzoeksgroepen hebben laten zien dat ook vestibulaire informatie verwerkt wordt in VIP. Alle data lijken erop te duiden dat VIP betrokken is bij het genereren van een driedimensionaal begrip van de orientatie van het lichaam in de ruimte.

De eerste doelstelling in dit onderzoek was de visuele component van VIP te vergelijken met de karakteristieken van de detectie van optische stroming in MST (Mediaal Superior Temporaal gebied). MST is een hersengebied dat sterk betrokken is bij de analyse van optische stroming en dat in tegenstelling tot VIP veel grondiger is onderzocht. De meeste neuronen in VIP lieten een duidelijke richtingsgevoeligheid zien, voor zowel translerende als expanderende, convergerende en roterende willekeurige puntpatronen en combinaties van deze (spiralen). In het bijzonder was VIP gevoelig voor expanderende patronen. Een opmerkelijke eigenschap van VIP-neuronen is dat de respons voor deze bewegende patronen blijft bestaan als deze verkleind op verschillende plaatsen binnen het receptieve veld (plaats op het netvlies waar bij het presenteren van een stimulus een neuron reageert) worden vertoond. Bijvoorbeeld een verkleinde optimale stimulus op slechts 1/9 deel van het receptieve veld genereerde nog steeds ongeveer 93 procent van de respons op een grote stimulus over het hele receptieve veld. Gemiddeld leverden stimuli die verkleind werden tot 1/9 deel van het totale receptieve veld ongeveer 64 procent van de respons over het hele veld. Om te testen of deze schaalinvariantie afkomstig was van de convergentie van kleinere translatie-gevoelige eenheden in een radiaal of circulair patroon ("mosaic hypothese") werd ook de voorkeursrichting voor translatie op deze deelgebieden van het receptieve veld gemeten. Het resultaat laat zien dat de voorkeursrichting voor translatie bij alle negen deelgebieden vrijwel hetzelfde is. Een neuron dat het best respondeert voor een expanderend patroon blijkt dus niet zijn informatie te krijgen van een groep richtingsdetectoren die zo georienteerd zijn dat ze vanuit het centrum naar buiten wijzen. Gebleken is dus dat de mosaic hypothese niet opgaat voor VIP. De respons lijkt te worden opgebouwd door kleinere detectoren met dezelfde eigenschappen als die voor het complete receptieve veld.

Omdat er voor MST neuronen waren gerapporteerd die reageerden op het kantelen van een vlak, werden de neuronen in VIP ook getest met dit soort optische stroming. In de literatuur wordt een optische stroming die overeenkomt met een fronto-parallel vlak dat om een fronto-parallelle as begint te roteren fanning genoemd. Neuronen in VIP bleken te reageren op fanning. In de meeste gevallen was de respons voor de optimale fanningsrichting ongeveer van dezelfde grootte als de optimale respons voor translatie, expansie/contractie en roterende patronen. Er werd dus geen speciale groep cellen gevonden die enkel reageert op het roteren van een vlak om een fronto-parallelle as. Voor de neuronen die gevoelig waren voor divergentie bleek de fanning respons in het algemeen goed verklaarbaar door het positioneren van het expanderende deel van de fanning-stimulus in het gevoeligste deel van het receptieve veld. De optimale richting voor de dots bewegend in een fanning patroon was meestal overeenkomstig de optimale translatierichting voor de dots. De conclusie is dat neuronen in VIP gevoelig zijn voor de beweging van vlakken, maar ze zijn niet gespecialiseerd in een dergelijke beweging.

Hoe lang moet een stimulus aangeboden worden voor dat de respons in de hersenen beginnen? Om deze vraag te beantwoorden voor VIP werden de stimuli aangeboden met een verschillende duur. De minimale duur die nodig is voordat een neuron respondeert

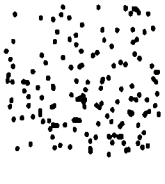


op een stimulus werd bepaald Het bleek dat voor bijvoorbeeld een expanderend patroon slechts 2 beeldjes van elk 17 milliseconden (ms) al een detecteerbare respons gaven (fasische respons, d w z kortduiende piek direct na de presentatie van de stimulus met een latentie van 60-120 ms) De respons verbeteerde bij het verlengen van de stimuli, tot 46 ms voor translatiestimuli en 118 ms voor expanderende patronen Voor de langer durende stimuli werd het tonische deel van de respons steeds belangrijker en liet dit deel vaak een sterkere richtingsselectiviteit zien dan het fasische deel van de respons De conclusie is dat de neuronen in VIP goed in staat zijn om ook patronen die slechts kort worden aangeboden te herkennen, maar dat het iets langer aanbieden mogelijk leidt tot een grotere nauwkeurigheid

Tot nu toe waren alle hier besproken stimuli van relatief korte duur (0 03 - 1 5 sec) en alle dots hadden een vaste snelheid Onder meer natuurlijke omstandigheden zijn de visuele patronen die wij zien meer complex en veranderen ze continu door onze eigen bewegingen Ook kunnen de stimuli elkaar snel opvolgen zoals bij oscillerende visuele patronen Dergelijke patronen werden ook aangeboden aan VIP neuronen, voornamelijk in de vorm van oscillerende translaties Het verschil tussen de respons voor beweging in de voorkeursrichting met de respons in de niet-voorkeursrichting (richtings "contrast") werd vergeleken voor oscillerende en niet oscillerende stimuli Dit verschil bleek veel groter te zijn voor oscillaties dan voor het sequentieel aanbieden (met pauses) van de translaties in de twee richtingen Voor een deel van de geteste neuronen bleek dat door dit mechanisme de maximale respons niet optreedt als de dots bewegen, maar juist als ze stilstaan (bij de overgang van beweging in één richting naar de andere richting) De reden hiervoor blijkt onder andere te zijn dat de respons door het vrijkomen van onderdrukking in de niet-voorkeurs richting kan samenwerken met de facilitatie van de respons voor de voorkeursrichting bij de oscillerende stimulus Zoook kunnen de inhiberende responsies voor de beide richtingen samenvallen en dit resulteert in een vergroting van het verschil in de respons tussen beide fases Elk neuron reageert met een vertraging op een stimulus Echter als de stimulus voorspelbaar was (bij de oscillaties) verscheen de respons toch steeds op dezelfde plaats ten opzichte van de komplete repetitie, en niet later als de cyclus korter duurde De bovengenoemde fase-afhankelijke respons was dus frequentie onafhankelijk (voor een bereik van 0 2 tot 6 0 repetities per seconde)

Verder bleek dat voor stimuli met constante-snelheid de fasische respons in de voorkeursrichting sterk kon domineren In een extreem geval nam deze fasische respons tijdens het oscilleren zo sterk af dat dit resulteerde in een omklappen van de voorkeursrichting Een neuron dat eerst reageert op een stimulus die naar rechts beweegt en niet op een stimulus die naar links beweegt, reageert op een oscillerende stimulus precies omgekeerd (reeds na een halve cyclus!) Het respondeert dan dus als de stimulus naar links beweegt en niet als de stimulus naar rechts beweegt

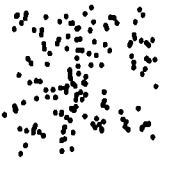
Een ander aspect van het detecteren van bewegingen is oogbewegingen Oogbewegingen helpen objecten te herkennen door ze te fixeren op het netvlies Verder kunnen ze de perceptie van eigen beweging op basis van optische stroming verstoren, tenzij de hersenen corrigeren voor de oogbewegingen Om dit te kunnen doen moeten de oogbewegingen en de informatie over de optische stroming worden gecombineerd Het was reeds bekend dat dit gebeurde in bijvoorbeeld MST De data in dit proefschrift laten



zien dat dit ook gebeurt in VIP. In VIP bevinden zich neuronen die responderen als het oog een volgbeweging maakt. Verder (zie hiervoor) responderen de meeste neuronen als er bewegende stimuli worden aangeboden. Het onderzoek beschreven in dit proefschrift heeft uitgewezen dat een (klein) deel van de neuronen reageert op beide modaliteiten.

In dit proefschrift wordt aangetoond dat de eigenschappen van de neuronen in VIP lijken op die in MST Verder laat deze studie zien dat er verrassende effecten kunnen optreden als er een nieuw soort stimulus wordt gebruikt. De respons op een oscillerend patroon kan niet voorspeld worden op basis van de respons op een traditionele set van stimuli (voorkeur- en niet-voorkeursrichting) met een constante snelheid in één richting. Dit laat zien dat de keuze van de stimuli in relatie tot de functie van het hersengebied van zeer groot belang is. De stimuli mogen niet te complex zijn gezien de meettijd die beschikbaar is om een enkel neuron te bestuderen, maar ze moeten complex genoeg zijn om iets te kunnen zeggen over de functie van het betreffende neuron.

Men heeft momenteel al een goede indruk van de verwerking van de informatie van bewegende stimuli en de plaats in de hersenen waar die informatie precies wordt verwerkt. Als we de in dit proefschrift (en in de literatuur) gebruikte eenvoudige stimuli vergelijken met de wereld om ons heen, zien we dat we slechts aan het begin staan van het begrijpen van de werking van de hersenen in het algemeen en van VIP in het bijzonder.



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Dit proefschrift zou nooit tot stand zijn gekomen zonder de hulp en steun van velen Allereerst is daar Jaak Duysens, die mij niet alleen op de tennisbaan bijschaafde, maar mij ook de elektrofysiologische technieken bijbracht Hij was altijd enthousiast voor een nieuw idee, maar probeerde mij tegelijkertijd te focussen op een haalbaar eindresultaat Stan Gielen, mijn promotor, dank ik voor zijn gestelde vertrouwen Hij nam het risico een kernfysicus met belangstelling voor neurale netwerken te laten werken met biologische natte netwerken van neuronen Hij gaf mij de vrijheid mijn eigen interesses te volgen terwijl tegelijkertijd zijn regelmatige checkups als 'advocaat van de duivel' zorgden voor een haalbaar einddoel

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Van Andre Minken en Jan van Gisbergen heb ik veel geleerd over hoe een wakkere aap getraind en neuronen bemeten moeten worden Verder wil ik bij deze mijn optische-stroming-goeroe Tjeerd Dijkstra bedanken, zijn archief en literatuurindex (hersenen) waren een onmisbare hulp bij de uiteindelijke keuze van stimuli en het schrijven van dit proefschrift Bas Neggers wil ik bedanken voor al het werk dat hij gedaan heeft Vooral toen het mij aan tijd begon te ontbreken om verder te werken aan de neurale netwerken was hij er enthousiast mee aan de slag

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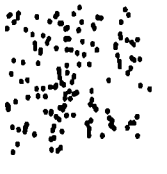
Al mijn collegae wil ik bedanken voor de uitstekende werk(?)sfeer Het verplichte volleybal (Thomo), koffiepauzes met verjaardagstaarten en het dagje uit waren altijd



zeer plezant. Verder verbreedden de tennis, questen en "grijze massa" collegae niet alleen mijn wetenschappelijke horizon

In het bijzonder wil ik Ger van Lingen bedanken voor al die babi pangangs die we hebben kunnen verorberen, Marc Theeuwen voor een constantere backhand en service en de familie Glasius voor de vele home cooked meals

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